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A REVISION OF STILLINGIA IN THE NEW WORLD*

DAVID JAMES ROGERS**

Three previous treatments of the genus *Stillingia* (Baillon¹, Mueller², Pax & Hoffman³) have done much to clarify the systematics of this group. However, these studies are based upon few specimens, little distribution data, and practically no habitat information. As a result, the species have remained conglomerate or split into ill-defined groups. An examination of annotations borne by herbarium specimens demonstrates the confusion concerning the identity of any one species. Furthermore, a clear differentiation has never been made between *Stillingia* and the closely neighboring genus *Sapium*, so that specimens collected without mature fruit can be assigned to neither with certainty.

Pax and Hoffmann³ have described twenty-six species of *Stillingia*; thirteen in North and Central America, nine in South America, three in Madagascar, and one in the Fiji Islands of the southern Pacific. The present revision undertakes to re-examine the American species with the purpose of effecting a natural organization. The standard methods of the herbarium systematist have been employed for interpretation of the species, amplified by special field studies for two of the species of the southeastern United States. A conservative concept of species is adopted, and no infra-specific entities are recognized where there are insufficient data for delimitation and description of the variants. Since none of the species of *Stillingia* are pantropic in distribution, no artificial separation is made by the omission of the species of the Eastern Hemisphere.

The great reduction of the floral organs not only in *Stillingia*, but in most genera of the Euphorbiaceae, limits the amount of emphasis which may be placed on the structures of the pistillate and staminate flowers for delimitation of the

¹Baillon, Étud. Gén. Euphorb. 510. 1858, ex parte.

²Muell. Arg. in DC. Prodr. 15²:1155. 1866.

³Pax & Hoffmann, in Engler, Pflanzenr. IV. Fam. 147. V:180. 1912.

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**Allegheny College, Meadville, Pennsylvania.

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species. This condition necessitates what may seem an over-emphasis on vegetative characters and differences of habitat and distribution. However, correlation of all factors demonstrates that those characters other than of the flower are of sufficient stability to justify their use in separation of species.

HISTORY

Stillingia was named by Garden⁴ in honor of Benjamin Stillingfleet, an English botanist who lived from 1702 to 1771. Endlicher⁵ first placed *Stillingia* in the Euphorbiaceae as a member of the tribe Euphorbieae.

J. F. Klotzsch⁶ placed the genus in the tribe Hippomaneae. His work included a study of South American representatives of several genera of Hippomaneae for which he gave a short description, usually followed by a list of species belonging to the genus. Klotzsch followed Endlicher in uniting *Sapium* and *Stillingia*, with *Sapium* as a section, maintaining *Stillingia* as the generic epithet. He gave a short description of *Stillingia*, followed by diagnoses of the sections EUSTILLINGIA and SAPIUM, but he listed no species for the genus.

Baillon's⁷ systematic studies on the Euphorbiaceae employed such a broad interpretation of genera allied to *Stillingia* that most of those genera of the presently recognized tribe Hippomaneae appeared as sections of *Stillingia*. In this work, he actually made no formal transfers, but merely listed the genera under the heading *Stillingia*. He apparently realized later⁸ that the names in his 'Étude Générale des Euphorbiacées' were not effectively transferred to *Stillingia* and tried to correct this situation in several volumes of 'Adansonia', in which he made the formal transfers, listed the basynoms, and cited specimens for each of his entities.

Mueller⁹ re-separated *Stillingia* and *Sapium*, and established *Gymnostillingia* as a separate genus, based on *S. acutifolia*. Later¹⁰ he reduced *Sapium* to the status of section in *Excoecaria*, but maintained both *Stillingia* and *Gymnostillingia* as separate genera.

Bentham¹¹ placed *Gymnostillingia* without rank within the genus *Stillingia*, recognizing for the first time that the gynobase is the most important generic character. Mueller¹⁰ had previously noted the occurrence of this structure, but failed to appreciate its importance as a linking character between *Stillingia* and *Gymnostillingia*. S. Watson¹² placed the herbaceous species of the southwestern United States and northern Mexico within the genus *Stillingia*, allied to *S. acutifolia*, but he did not definitely state whether these species should be treated as a section or as a subgenus. Pax and Hoffman¹³ established a new section, LEPTO-

⁴Garden ex L. Mant. 19. 1767.

⁵Endlicher, Gen. Pl. 2:1110. 1836-1840, ex parte.

⁶Klotzsch, in Wieg. (Erichs.) Arch. 7:187. 1841.

⁷Baillon, Étud. Gen. Euphorb. 510. 1858, ex parte.

⁸Baillon in Adansonia 1:350. 1861; 2:27. 1861; 3:162. 1862; 5:320. 1865.

⁹Muell. Arg. in Linnaea 32:87. 1863.

¹⁰Mueller, in DC. Prodr. 15²:1155. 1866.

¹¹Bentham in Benth. & Hook. f. Gen. Pl. 3:334. 1880.

¹³Pax and Hoffmann, in Engler, Pflanzenr. IV. Fam. 147. V:194. 1912.

STACHYAE, for these four species.

Pax and Hoffman¹⁴ were the first to divide the tribe Hippomaneae; *Stillingia* appears as a member of the subtribe Stillingiinae. These authors have given the limits of the genus as it is known today, dividing it into six sections based largely on vegetative characters.

I have not altered the generic limits of *Stillingia* since there is no confusion with the allied genera. Within the genus, however, new subgeneric categories are employed to emphasize the relationships and differences between the species groups. The subgenus is used in order to demonstrate a wide morphological divergence of two large species groups, and the series is used in an effort to show that boundaries between the groups within the subgenus are not distinct, and are at best tendencies toward morphological divergences. This seems to be a more logical division than to place all of the species groups on one level (as sections), indicating nothing of the stages of differentiation on a scale above the species.

GENERIC RELATIONSHIPS

Within the tribe Hippomaneae, *Sebastiania*, *Excoecaria*, *Maprounea*, and *Sapium* are the genera which have been most frequently confused with, and seem to be the most closely related to *Stillingia*. I am not prepared to comment upon the correct phylogenetic sequence of these genera, nor upon the position of *Stillingia* with reference to them. The genus *Sapium* has the closest morphological resemblance to *Stillingia*, and there has been some confusion in the past concerning the characters which separate these two genera. In *Stillingia*, an abscission layer forms above the base of each of the cocci so that after dehiscence, a three- or two-rayed hardened portion of the pericarp remains attached to the pedicel. The hardened portion of the pericarp, called the gynobase in this study, is the most prominent distinguishing feature of *Stillingia*. None of the other genera have this structure.

It is slightly more difficult to separate *Stillingia* from *Sapium* when flowering specimens without mature fruits are available. The following list of characters will serve to differentiate the two genera with ease when all of the characters are considered together (cf. fig. 1). Any one of these may fail if taken individually:

Stillingia

Sapium

Pistillate Flower

Sepals separate (except in *S. saxatilis*), or absent.

Sepals united.

Seed

Testa hardened, smooth to rugulose, not arillate.

Testa arillate in American species.

Vegetative Characters

Herbs, shrubs, or occasionally small trees.

Large trees, infrequently subshrubs.

Glands at base of leaf present or absent, rarely elongate, cyathiform or scutelliform, the opening of the glands wide, irregularly to regularly spaced.

Glands at base of leaf mostly present, mostly elongate, tubiform or urceolate, the opening constricted, usually opposite, more a part of the petiole than of the leaf blade.

¹⁴Pax and Hoffmann, loc. cit. 180. 1912.

The three remaining genera are easily distinguished from *Stillingia*: *Sebastiania* and *Excoecaria* by the three to several stamens of the staminate flower, pistillate flower long-pedicellate, sepals united, gynobase absent; *Maprounea* by its compact inflorescence which appears almost as a capitulum, pistillate flower long-pedicellate, without gynobase.

The following is a synopsis of *Stillingia* in the Western Hemisphere, as projected in this study.

Subg. STILLINGIA	Series OPPOSITIFOLIAE	1. <i>S. oppositifolia</i> Baill. ex Muell. Arg. 2. <i>S. Bodenbenderi</i> (O. Ktze.) D. J. Rogers 3. <i>S. peruviana</i> D. J. Rogers 4. <i>S. sanguinolenta</i> Muell. Arg. 5. <i>S. microsperma</i> Pax & Hoffm. 6. <i>S. diphterina</i> D. J. Rogers 7. <i>S. bicarpellaris</i> S. Wats. 8. <i>S. aquatica</i> Chapm.
	Series DICHOTOMAE	9. <i>S. Uleana</i> Pax & Hoffm. 10. <i>S. trapezoides</i> Ule 11. <i>S. dichotoma</i> Muell. Arg. 12. <i>S. saxatilis</i> Muell. Arg.
	Series SYLVATICAE	13. <i>S. salpingadenia</i> (Muell. Arg.) Huber 14. <i>S. scutellifera</i> D. J. Rogers 15. <i>S. Dusenii</i> Pax & Hoffm. 16. <i>S. zelayensis</i> (HBK.) Muell. Arg. 17. <i>S. texana</i> I. M. Johnst. 18. <i>S. sylvatica</i> Garden ex L.
Subg. GYMNSTILLINGIA	Series ACUTIFOLIAE	19. <i>S. acutifolia</i> (Benth.) Benth. ex Hemsl.
	Series TRECULIANAE	20. <i>S. Treculiana</i> (Muell. Arg.) I. M. Johnst. 21. <i>S. paucidentata</i> S. Wats. 22. <i>S. spinulosa</i> Torr. 23. <i>S. linearifolia</i> S. Wats.

SYSTEMATIC CRITERIA

The genus *Stillingia* is a diverse group of perennial herbs, subshrubs, shrubs, and small trees. The tree habit is rare in the American species: *S. acutifolia*, of southern Mexico and Guatemala, and *S. oppositifolia*, of southeastern Brazil, are the only species which have sufficient height and diameter of trunk to be called trees.

Stems of the species of all series except SYLVATICAE arise directly from a tap root. Although seldom found on herbarium specimens, the woody root crown or rhizomes of species of SYLVATICAE are, nevertheless, of diagnostic value. The adventitious roots of *S. sylvatica* and *S. aquatica* are distinctive, those of the former being stoutly elongate-fusiform, arising at wide intervals along the rhizome, and those of the latter filiform and very closely set on the primary root.

The branching systems are opposite, alternate, approximate, or fascicled, the latter being a result of shortened internodes subtending the inflorescence and thus presenting a somewhat whorled appearance. The fascicled branching pattern gives the upper portions of the plant a corymbiform appearance. The bark of the

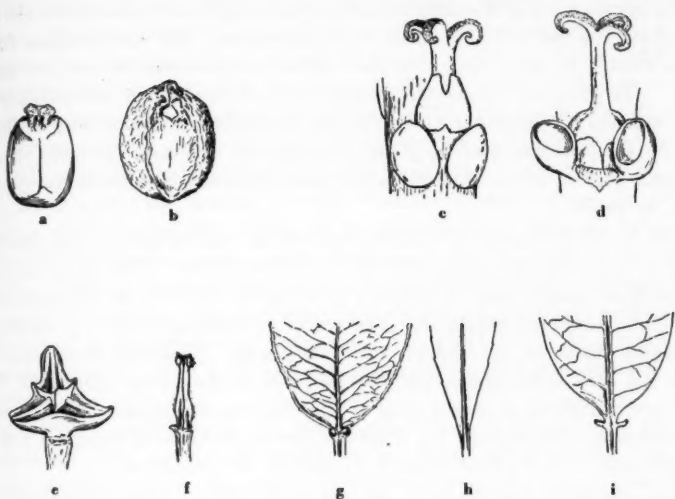


Fig. 1. Illustrations of taxonomic criteria for *Stillingia* and *Sapium*.

Seed: a—*Stillingia scutellifera*, testa hardened; b—*Sapium haematospermum*, testa arillate.

Pistillate flower: c—*Sapium marginatum*, the sepals united; d—*Stillingia salpingadenia*, the sepals separate.

Pedicel after dehiscence of fruit: e—*Stillingia sylvatica* ssp. *sylvatica*, the gynobase present; f—*Sapium sebiferum*, without gynobase.

Leaf: g—*Stillingia scutellifera*, with 2 basal scutelliform or cyathiform glands; h—*Stillingia aquatica*, without glands at base of blade; i—*Sapium pedicellatum*, with 2 basal, tubular glands.

shrubby species is lenticellate in varying degrees, with the exception of those of series DICHOTOMAE, whose succulent species have no lenticels. *S. sanguinolenta* has an unusually rough bark due to the presence of a large number of lenticels. Succulence of stem and leaf is a definitive character of the species of series DICHOTOMAE.

The leaves are widely spaced on the stem, except in *S. Bodenbenderi* and *S. peruviana*. In these species the leaves may be widely spaced but frequently they may arise in groups on peg-like short shoots. The outline, margin, venation, and texture of the leaves are important key characters. The leaves of the Mexican, Central and South American species of the subgenus *STILLINGIA*, with few exceptions, are provided with two to several cup- or boat-shaped glands at the base of the blade. This is not a constant feature of each leaf, but generally more than one leaf of a standard herbarium specimen will have these modified serrations. The types of leaf texture occurring in *Stillingia* are: thin to firmly membranaceous, definitely coriaceous, and succulent or fleshy. These conditions are usually characteristic of whole groups of species, but *S. diphterina* is the only known species with coriaceous leaves.

The organization of the inflorescence, a spiciform thyrs, is essentially the same throughout the genus. The flowers are monoecious, with the pistillate flowers always solitary in the cymule, but the number of staminate flowers in a cymule varies. The pistillate flowers are attached toward the base of the peduncle and either immediately subadjacent to the lowest staminate cymule or with a distinct space on the peduncle separating the pistillate and staminate cymules. The inflorescence may be pedunculate below the point of insertion of the lowest pistillate flower, or sessile.

Both the pistillate and the staminate cymules are subtended by a bract the shape of which is of some importance in species differentiation. The bracts are squamaceous in all species except *S. Dusenii*, in which the bract of the pistillate cymule seems to be somewhat foliaceous. The bracts are subtended by two patelliform, cyathiform, tubiform, or urceolate marginal glands. Generally, these glands are simple, but in *S. oppositifolia* they may be twice or three times branched. These glands are considered as homologues of the cup-shaped serrations at the base of the leaves of several species. The staminate flowers are borne in groups of 3 to 13, or singly in the axil of a bract toward the apex of the inflorescence.

This inflorescence structure is assumed to be derived from a more primitive type by reduction. The inflorescence structure of *Hevea*, for example, with several pistillate flowers on the primary and secondary axes, might represent a more primitive condition than that observed in *Stillingia* where the pistillate flowers are single in the cymules. A further reduction series is evident within the genus *Stillingia* in the staminate cymule structure. The species of subgenus STILLINGIA are characterized by three to many staminate flowers in each cymule, but the subgenus GYMNSTILLINGIA has only one staminate flower for each cymule.

A strengthening feature for the distinction between the two subgenera is found in the sepals of the pistillate flower. All of the species of subgenus STILLINGIA have three (or two in *S. bicarpellaris*) sepals which are distinct, or fused into a truncate annulus in *S. saxatilis*, and the remnants of these are occasionally apparent at the base of the gynobase even at maturity of the fruit. The name GYMNSTILLINGIA is derived from the absence of a calyx, and all species of the subgenus except *S. acutifolia* are completely lacking it. *S. acutifolia* is a transitional species in this respect, with very small and fugacious sepals.

No primary systematic importance has been attached to the staminate flowers since they are rather uniform and present no readily observed differences. On the other hand, relative congestion of the staminate cymules and the total number of staminate flowers of an individual cymule are used in the diagnostic treatment. The pollen grains are spheroid or nearly so, with three pores, except in species of series DICHOTOMAE in which they are ellipsoid with one lateral pore.

The mature fruit of *Stillingia* affords the most striking feature of generic distinction, but presents few characters for species diagnosis. The gynobase (described

in the section on Generic Relationships) is a constant feature of all species of *Stillingia*. The lobe length of the mature gynobase is consistently given in the descriptions, being measured from the central column to the apex of the lobe. The variability of this character within a species prevents inclusion as a key character.

Seed size, contour, and surface are constant within the species, for the most part. Again, variation occurs notably in the extreme southeastern part of the range of *S. sylvatica* where introgression with *S. aquatica* is reflected in the variability of the seed. The presence or absence of the caruncle is one of the best supporting characters for the division of the genus *Stillingia* into two subgenera. Subgenus STILLINGIA is characterized by the presence of a well-defined caruncle in all species. Subgenus GYMNSTILLINGIA is not completely without this body, however, and a very definite caruncle appears in *S. Treculiana*. *Stillingia acutifolia*, *S. spinulosa*, and *S. linearifolia* are ecarunculate; *S. paucidentata* is a transitional species in this respect, with a very minute and fugacious, but nevertheless definite caruncle.

Attempts to count the somatic chromosomes of *S. sylvatica* using Perry's¹⁵ techniques were not particularly successful, but were sufficiently good to show that a number in excess of that reported by Perry ($2n = 36$) were present in the specimens examined. Since this might indicate a polyploid race within the species *S. sylvatica*, an effort to correlate pollen grain size with polyploidy was made. Although there was some variability in pollen grain dimensions, there was no indication of two different races, the range of variation being continuous.

SUBGENERIC CATEGORIES

The subgenus STILLINGIA includes those species with 3 to 13 staminate flowers in a cymule, 3 to 2 definite sepals in the pistillate flowers, and a well-defined caruncle on the seed. Species with a single staminate flower in a cymule, sepals and caruncle absent, are referred to subgenus GYMNSTILLINGIA. There is a sufficient overlap of characters between the two subgenera, however, to prevent the establishment of distinct genera.

The series within both subgenera are divided largely on vegetative characters with only a few correlating floral characters. In subgenus STILLINGIA the first and most primitive series, OPPOSITIFOLIAE, is a group of woody shrubs or small trees with membranaceous or coriaceous leaves and spheroid pollen grains. The individual species of this series are quite distinct morphologically.

Series DICHOTOMAE, a group of four shrubby species, is characterized by mostly succulent stems and leaves, and by ellipsoid pollen grains with one pore. This interesting group is poorly known and infrequently collected. *Stillingia Uleana* seems to be the connecting species between the species of series DICHOTOMAE and those of OPPOSITIFOLIAE. Further collections from eastern Brazil, to which region this group is confined, may throw more light on the inter-relations of these species.

¹⁵Perry, in Am. Jour. Bot. 30:527. 1943.

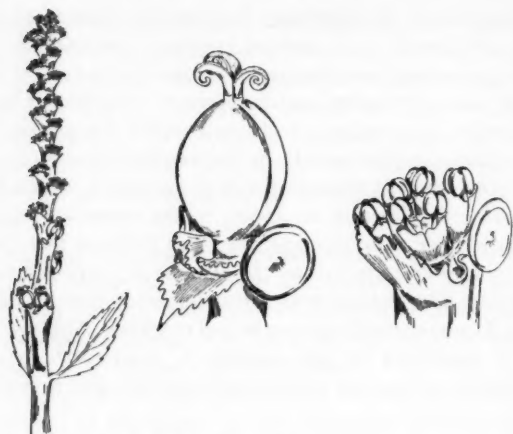


Fig. 2. Inflorescence and flower structure of *Stillingia zelayensis*, typical of subgenus *STILLINGIA*.

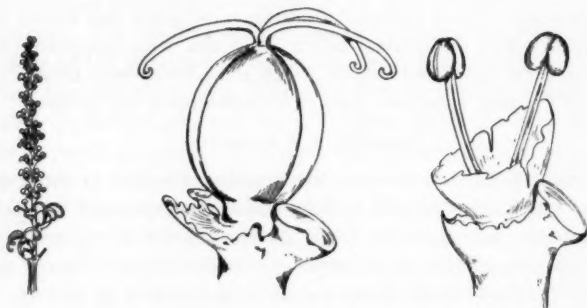


Fig. 3. Inflorescence and flower structure of *Stillingia paucidentata*, typical of subgenus *GYMNOSTILLINGIA*.

The third series of subgenus *STILLINGIA*, *SYLVATICAE*, is composed of the best known and most extensively collected group of species within the genus *Stillingia*. This series represents a different type of specialization from that of series *DICHOTOMAE*. All of the species are suffruticose, but their floral structure is very similar to that of the less specialized species of *OPPOSITIFOLIAE*, from which this group seems to be derived. Although the species are very closely related, they seem to have diverged and stabilized themselves sufficiently to be called species rather than subspecies of one large "cenospecies". Evidence of their close relation is seen not only in morphological characters, but also in the fact that they have apparently erected none or few genetic barriers to prevent rather free hybridization where their geographic margins overlap. Because of these putative hybrids, many names

have been applied previously without any thought as to the explanation of the phenomenon, nor of the ensuing confusion.

The three South American representatives of SYLVATICAE, *S. salpingadenia*, *S. scutellifera*, and *S. Dusenii*, are widely separated geographically from the three North American species. Although easily distinguished morphologically from *S. sylvatica* of the southern United States, *S. scutellifera* resembles the Texan representative of the former in many particulars, both ecologically and morphologically.

In only one case have I seen fit to designate a subspecies in this series, that of *S. sylvatica* ssp. *tenuis*, which occurs only in extreme southeastern Florida. Sufficient material, together with personal knowledge of the habitat through field studies, makes this possible. There seems little doubt, however, that at least one species in South America, *S. scutellifera*, has a closely related form, exemplified by Hassler 5612 and called *saxatilis* var. *salicifolia* by Chodat and Hassler¹⁶, which possibly could be designated as a subspecies. Lack of sufficient knowledge makes such a step premature.

There seems to be little or no genetic barrier between *S. aquatica* of Series OPPOSITIFOLIAE and *S. sylvatica* of Series SYLVATICAE. In the spring of 1950 local population samples were made at several points in Florida to determine the possibility of hybridization between such widely differentiated species. The assembled specimens were studied and indexed according to techniques used by Anderson¹⁷. Although larger samples would have been desirable, those actually made give rather positive evidence that free hybridization does occur.

The subgenus GYMNSTILLINGIA is composed of two series which are widely differentiated. Series ACUTIFOLIAE has one shrubby species, *S. acutifolia*, with broad, thinly membranaceous leaves. The second series, TRECULIANAE, is a group of perennial herbs with a compact growth habit and for the most part very small, narrow leaves. There seems little doubt that the four species of this series form a natural group of plants which have become adapted to the extreme environmental conditions under which they exist.

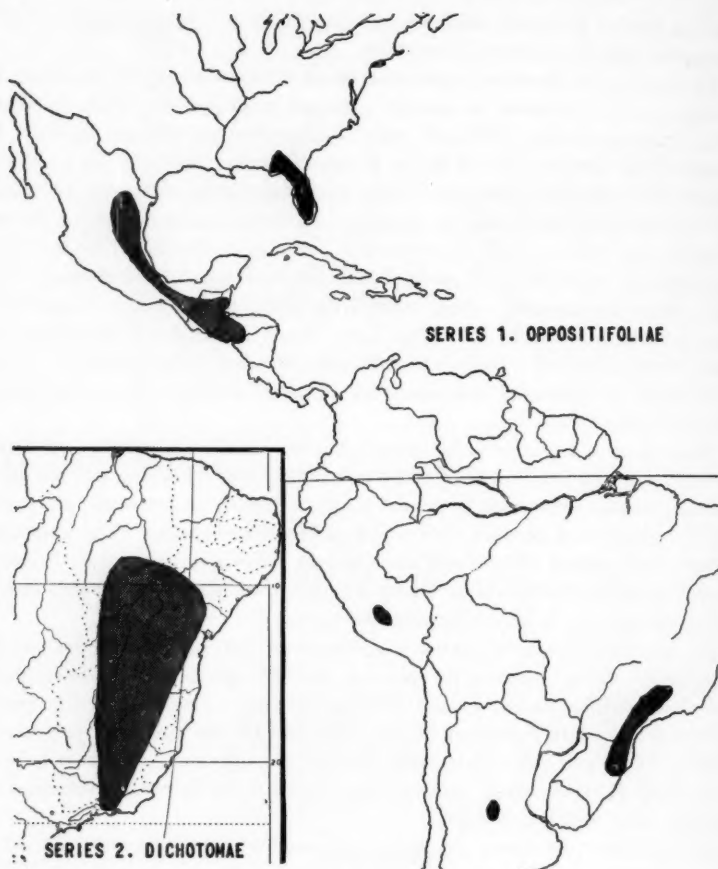
GEOGRAPHY

In the accompanying maps (figs. 4 and 5) are shown the known areas of distribution of the species of *Stillingia* in the New World. In general, the North American material has been sufficiently ample to plot distributions with some accuracy, but there are still many gaps and disjunctions which may be filled with further collecting, particularly in Central and South America.

For the most part, the species of *Stillingia* are limited to areas of temperate or subtropical climate, those occurring closest to the equator being at higher altitudes. In South America, *S. Bodenbenderi* reaches farthest south, in the Sierra de Cordoba in Argentina; *S. sylvatica* is the most northern species in North America, reaching the 38th parallel in southern Kansas.

¹⁶Chodat & Hassler, in Bull. Herb. Boiss. II, 5:676. 1905.

¹⁷Anderson, Edgar. Introgressive Hybridization. New York. 1949.

Fig. 4. Ranges in *Stillingia*.

Although the series *OPPOSITIFOLIAE* is very widely distributed in both continents, the individual species normally occupy small ranges. With the exception of *S. aquatica* the species of this series are found in mountainous regions in mesophytic habitats, mostly at altitudes above 500 meters. They generally occupy land masses of both continents which have been the longest exposed and the longest continuously available for plant growth (Weeks¹⁸, Schuchert¹⁹). *Stillingia aquatica*, on the other hand, is the only species of the genus found in marshy or swampy habitats only a few meters above sea level in a region of relatively recent origin.

¹⁸Weeks, in Bull. Geol. Soc. Am. 59:249. 1948.

¹⁹Schuchert, Historical Geology of the Antillean-Caribbean Region. New York. 1935.

Fig. 5. Ranges in *Stillingia*.

The species of Series DICHOTOMAE are found only in the dry, upland regions of eastern Brazil. Their areas of distribution are the least understood of any in *Stillingia*. At least one species, *S. trapezoidea*, occurs in the *caatinga*, or open scrub forest of southern Piauh, Brazil. The exact type of habitat is not known for the other three species of this series, but their adaptation to a dry habitat is shown in succulence of stem and leaf; this, together with their locality, marks them as a derived group.

With the exception of *S. zelayensis* of the Mexican and Central American highlands, species of the series SYLVATICAE are found in regions of lower elevation than

those of series OPPOSITIFOLIAE, generally from near sea level to altitudes of 300-500 m. *Stillingia zelayensis*, however, is confined to upland regions, from 1200 to 2800 m., mostly in open pine forests. The greatest distribution areas of the species of this series are in regions which were inundated by Cretaceous seas, and which today are mostly covered with open forests or savannas in North and South America.

Stillingia acutifolia, the only species of series ACUTIFOLIAE, occupies a small area in southern Mexico and Guatemala. It occurs in the mountainous regions, within a definite mesophytic habitat. The four species of series TRECULIANAE are rather narrow endemics in the arid desert or semi-desert regions of the southwestern United States and northern Mexico.

STUDY MATERIAL

The herbaria where specimens have been obtained for study, together with the symbols²⁰ employed in their citation, are as follows:

- A—Arnold Arboretum of Harvard University, Jamaica Plain, Mass.
- AN—Colegio Anchieta, Porto Alegre, Brazil.
- BR—Jardin Botanique de l'État, Bruxelles.
- C—Universitetes Botanisk Museum, Copenhagen.
- F—Chicago Natural History Museum (Field Museum).
- FLAS—Agricultural Experiment Station Herbarium, University of Florida, Gainesville.
- G—Institut de Botanique Systematique de l'Université, Genève.
- GH—Gray Herbarium of Harvard University, Cambridge, Mass.
- K—Royal Botanic Gardens, Kew.
- LIL—Instituto Miguel Lillo, Tucumán, Argentina.
- MICH—University of Michigan, Ann Arbor.
- MO—Missouri Botanical Garden, St. Louis.
- NY—New York Botanical Garden.
- OKL—Bebb Herbarium, University of Oklahoma, Norman.
- P—Muséum National d'Histoire Naturelle, Paris.
- S—Naturhistoriska Riksmuseet, Stockholm.
- TEX—University of Texas, Austin.
- UC—University of California, Berkeley.
- US—United States National Herbarium, Smithsonian Institution, Washington, D. C.

I wish to acknowledge my indebtedness to the curators of these institutions, and to the Director and Staff of the Missouri Botanical Garden where this study was made.

²⁰The symbols used are as suggested by Lanjouw in Chron. Bot. 5:143. 1939.

TAXONOMY

STILLINGIA Garden, ex L. Mant. 19. 1767; Baillon, Étud. Gén. Euphorb. 510. 1858, ex parte; Muell. Arg. in DC. Prodr. 15²:1155. 1866; Benth. in Benth. & Hook. f. Gen. Pl. 3:334. 1880; Pax, in Engl. & Prantl, Nat. Pflanzenf. III, 5:96. 1890; Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147. V:180. 1912.

Seborium Raf. Sylva Tellur. 63. 1838.

Ditrisynia Raf. loc. cit. 64. 1838.

Glabrous perennial herbs, shrubs, or small trees. Leaves simple, alternate, opposite, or verticillate, usually with 2 to several filiform, glandular stipules, entire to serrate, with or without 2-3 cyathiform or scutelliform glands at base of blade, the serrations glandular or occasionally the glands in the sinuses of the serrations. Inflorescence a terminal, spiciform thyrse, the cymules bracteate, the bracts with 2 marginal glands; flowers monoecious, monochlamydeous or naked. Pistillate flowers solitary, borne toward the base of the peduncle; sepals 3, rarely 2, mostly separate, infrequently united into a truncate annulus, imbricate, or the sepals absent; ovary superior, 3- to 2-celled, a single pendulous, anatropous ovule in each cell; stigmas 3, rarely 2, recurved, more or less coalescent at the base into a single style. Staminate flowers solitary or 3-13 in a cymule, occupying the upper portion of peduncle, the 2-lobed calyx always present; stamens 2, exserted, the filaments coalescent at the base, the 2 thecae adnate, extrorse, longitudinally dehiscent; pollen spheroid to ellipsoid, with 1-3 pores, the exine reticulate, granular, or punctate. Fruit a 3- to 2-celled, dry, septically dehiscent capsule, the accrescent gynobase 3- to 2-lobed, hardened and persistent after dehiscence of carpels; seeds 1 in each carpel, with or without a micropylar caruncle, the embryo central, the cotyledons broad and flattened, the endosperm mealy.

Standard species: *Stillingia sylvatica* Garden, ex L. Mant. 19. 1767.

KEY TO THE SUBGENERA AND SERIES

- A. Staminate flowers in clusters of 3 or more; sepals of pistillate flowers present, persistent; caruncle present.....Subgen. I. *STILLINGIA* (p. 220)
- B. Shrubs or small trees arising from a tap root; stems perennial, woody or succulent, older parts gray-brown and frequently somewhat blackened, lenticels frequently obvious.
 - C. Stems woody; leaves membranaceous or coriaceous; pollen spheroid, with 3 pores; tropical and subtropical Americas, exclusive of eastern and northeastern Brazil.....Ser. 1. *OPPOSITIFOLIAE* (p. 220)
 - CC. Stems mostly succulent; leaves succulent; pollen ellipsoid, with 1 lateral pore; eastern and northeastern Brazil.....Ser. 2. *DICHOTOMAE* (p. 230)
- BB. Subshrubs arising from an enlarged woody base; stems mostly annual or biennial, herbaceous or subherbaceous, green to reddish-brown, usually without lenticels.....Ser. 3. *SYLVATICAE* (p. 233)
- AA. Staminate flowers single; sepals of pistillate flowers absent, or minute and fugacious; caruncle absent (except in *S. Treculiana* and *S. pseudentata*).....Subgen. II. *GYMNOSTILLINGIA* (p. 243)
 - D. Shrubs or small trees, leaves distinctly petiolate, the pinate venation prominent; mesophytic habitats, Central America.....Ser. 4. *ACUTIFOLIAE* (p. 243)
 - DD. Perennial herbs; leaves sessile to subsessile, the venation not prominent (except *S. spinulosa* with palmate venation); xerophytic habitats, southwestern United States and northwestern Mexico.....Ser. 5. *TRECVLIANAE* (p. 245)

Subgenus I. STILLINGIA

§ *Eustillingia* Kl. in Wieg. (Erichs.) Arch. 7:187. 1841; emend. Muell. Arg. in Linnaea 32:87. 1863.

Series 1. OPPOSITIFOLIAE D. J. Rogers, ser. nov.

§ *Fruticosae* Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:186. 1912.

Caules lignosi; folia membranacea vel coriacea; pollen sphaeroideum, foraminibus 3. Americae tropicae et subtropicae Brasilia orientali excepta.

KEY TO THE SPECIES

- A. Leaves usually broadest at the middle or above; secondary roots widely spaced on the primary, not thickly set; seeds ellipsoid to ovoid, 3-6 mm. long, rugulose or smooth; tropical and subtropical America, exclusive of the United States, on well-drained soils.
 - B. Pistils 3-carpellate; leaves narrowly to broadly elliptic; seeds relatively small, 5 mm. long or less.
 - C. Inflorescence sessile below the lowest pistillate cymule, the cymules decussate; glands of pistillate bracts frequently trifurcate; leaf margins finely to coarsely serrate; branches strictly dichotomous, never fascicled; southeastern Brazil..... 1. *S. oppositifolia*
 - CC. Inflorescence pedunculate below the lowest pistillate cymule, the cymules spiral; glands of pistillate bracts simple; leaf margins finely and evenly serrulate; branches not always strictly dichotomous, sometimes fascicled.
 - D. Leaves arising in groups on peg-like short shoots, or alternate if solitary; South America.
 - E. Leaves short-petiolate to subsessile; bracts of staminate cymules without mucro; Argentina and Brazil..... 2. *S. Bodenbenderi*
 - EE. Leaves relatively long-petiolate; bracts of staminate cymules mucronulate; Peru..... 3. *S. peruviana*
 - DD. Leaves solitary and opposite, arising on main axis; Mexico and Central America.
 - F. Bark densely lenticellate; branches opposite or occasionally approximate, never fascicled; fruit deeply 3-lobed; Mexico.. 4. *S. sanguinolenta*
 - FF. Bark sparsely lenticellate; branches frequently fascicled; fruit shallowly 3-lobed; Central America.
 - G. Leaves acuminate, membranaceous, 8-13 cm. long, 2-4 cm. broad; petioles 0.5-1.0 cm. long; inflorescence crowded, the cymules congested, relatively many-flowered..... 5. *S. microstigma*
 - GG. Leaves acute, coriaceous, 1.8-3.5 cm. long, 0.5-2.0 cm. broad; petioles short, 0.1-0.3 cm. long; inflorescence open, the cymules distant, relatively few-flowered..... 6. *S. diphterina*
 - BB. Pistils 2-, rarely 3-carpellate; leaves linear-lanceolate; seeds larger, 6 mm. long..... 7. *S. bicarpellaris*
 - AA. Leaves usually broadest toward the base; secondary roots closely set on the primary, forming a dense mat; seeds subspherical, 2-3 mm. in diameter, rugose; Georgia and Florida, in swampy places or shallow intermittent ponds..... 8. *S. aquatica*
1. *STILLINGIA OPPOSITIFOLIA* Baill. ex Muell. Arg. in DC. Prodr. 15²:1160. 1866. (T.: Sellow 4985!).

Shrubs or small trees 1-5 m. tall; stems woody, frequently branched, the branches opposite, terete, slender, sparsely lenticellate, gray-brown, frequently somewhat blackened on older parts. Leaves decussate, widely spaced, petiolate, membranaceous, yellowish-green, elliptic or spatulate to narrowly rhombic, 3-9

cm. long, 1-5 cm. broad, apex rounded to acute or acuminate, base acute, cyathiform glands infrequent, finely to coarsely serrate, the midrib prominent, secondary venation not obvious; petiole 0.3-1.2 cm. long, sulcate above. Inflorescence 1-2 cm. long, usually sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules decussate, crowded, distinctly separate upon the peduncle; bracts of pistillate cymule caudate-acuminate, the staminate broadly rhombic, with 3 mucros, the glands urceolate, the pistillate frequently trifurcate. Sepals of pistillate flower 3, linear-lanceolate, 2 mm. long or less; ovary sessile, 3-carpellate; styles 2-3 mm. long. Staminate cymules 3- to 5-flowered, the flowers subsessile, about 1-2 mm. long; calyx shallowly 2-lobed, the lobes entire; pollen spheroid, with 3 pores, the exine coarsely reticulate. Fruit deeply 3-lobed, about 5-6 mm. wide, the lobes of the gynobase 2-3 mm. long, seed not seen.

A common shrub in *Araucaria* woods, between 600 and 1000 m. alt., with average rainfall of 1750 to 2500 mm., 15-17° C. average temperature, with occasional snowfall and -5° C. during winter. Flowers and fruits from October to March.

BRAZIL: MINAS GERAIS: ad Lagoa Santa in silvis super rupes calcar., *Warming* 1525 (C, G, GH). RIO GRANDE DO SUL: Montenegro, S. Salvador, *Friedrichs* 32938 (LIL, S); San Francisco de Paula, *Rambo* 2278 (LIL), *Rambo* 44828, 46236 (AN); Kappesberg, pr. Montenegro, S. Salvador, in silva, *Rambo* 2278 (AN, LIL), *Rambo* 43828 (AN); Passo do Inferno, pr. San Francisco de Paula, *Rambo* 4818, 4824 (AN); Nova Petropolis, pr. Cai, *Rambo* 6575 (AN); Nonoae ad fl. Uruguay superius, ad araucarietum, *Rambo* 28353 (AN, MO); Caracol, pr. Canela, *Rambo* 28809 (AN); San Francisco de Paula, Vila Oliva, in silva, *Rambo* 31144 (LIL); Bom Jesus, Fazenda Bernardo Velho, in silva campestri, *Rambo* 34775 (AN, LIL, S); Vila Oliva pr. Caxias, *Rambo* 43136 (AN); Gramado, pr. Canela, *Rambo* 44985 (AN). WITHOUT LOCALITY: "Brasilia meridionali", *Sellow* (Sello) 4985 (G, K, P).

I am indebted to Fr. Rambo for his data on the habitat and distribution of this species.

Baillon²¹ published *Stillingia oppositifolia* Kl. as a *nomen nudum*, apparently taking this name from a specimen in the Berlin Herbarium annotated *Sapium oppositifolium* by Klotzsch. In the Atlas published with his *Étud. Gén. Euphorb.*, Baillon designates the illustrations of Plate V, figs. 24 and 25 as *Stillingia* (*Sapium*) *oppositifolia* Kl. However, in the text (p. 513) he lists *S. oppositifolium* Kl. together with ten other species in which the "S" clearly stands for *Sapium*, since the endings of the specific epithets agree with the endings of the neuter noun *Sapium* and not with the feminine *Stillingia*. Of the ten other species listed on page 513 of the text, two are designated in the Atlas as *Sapium*. Baillon's taxonomy includes all of these species under *Stillingia*, but he apparently did not make the necessary transfers in nomenclature. The name *Stillingia oppositifolia* was validated by Muell. Arg. in DC. Prodr. 15²:1160. 1866.

²¹ Baillon, *Étud. Gén. Euphorb.* 513. 1858.

2. *STILLINGIA Bodenbenderi* (O. Ktze.) D. J. Rogers, comb. nov.

Sapium Bodenbenderi O. Ktze. Rev. Gen. 3²:292. 1898. (T.: *Bodenbender* 6902!).

Excoecaria Bodenbenderi (O. Ktze.) K. Schum. in Just's Bot. Jahresb. 26¹:349. 1898.

Sapium subsessile Hemsl. in Hook. Icon. Pl. t. 2684. 1901. (T.: *Weir* 315).

Shrubs or small trees; stems woody, frequently branched, the branches alternate, opposite or approximate, sometimes fascicled, terete, slender, moderately lenticellate, gray or slightly reddish-brown. Leaves clustered on short side branches, alternate if single, crowded, subsessile, stiffly membranaceous, elliptic to obovate, 0.8–3.0 cm. long, 0.5–1.3 cm. broad, apex acute to rounded, base acute, usually with 2 cyathiform glands, callose-serrulate, the midrib prominent, the secondary venation obscure. Inflorescence 1–2 cm. long, slightly flexuose, the peduncle elongate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, widely spaced, not distinctly separate upon the peduncle; bracts of the pistillate cymule elliptic, mucronate, the staminate elliptic to ovate, rounded to acute, the glands patelliform. Sepals of pistillate flower 3, elliptic, mucronate; ovary sessile, 3-carpellate; styles unknown. Staminate cymules 5- to 9-flowered, the flowers subsessile; calyx shallowly 2-lobed, the lobes serrulate; pollen irregularly ovoid, with 3 pores, the exine reticulate to granular. Lobes of the gynobase 2–3 mm. long. Fruit and seed not seen.

ARGENTINA: CORDOBA: Sierra de Córdoba, Sept., *Bodenbender* 6902 (NY, photo in F); Dept. de las Minas, Cuesta de las Chacras, Jan. 14, *Hieronymus* 817 (G, NY, US).

Hemsley's failure to recognize the affinities of his *Sapium subsessile* with *Sapium Bodenbenderi* O. Ktze. probably is due to the fragmentary nature of Bodenbender's specimens. The plate of *Sapium subsessile* (in Hook. Icon. Pl. t. 2684. 1901), however, indicates that Hemsley's species is synonymous with *Sapium Bodenbenderi* and, furthermore, that the specimen is *Stillingia*, not *Sapium*. These drawings show a calyx of three separate sepals and a leaf base with cyathiform glands, both of which are characteristic of *Stillingia* rather than *Sapium*. In addition, the collection of Hieronymus (no. 817), referred by Hemsley to *Sapium subsessile*, possesses a gynobase, one of the best morphological distinctions of *Stillingia*. Huber, in an appendaged note in Bull. Herb. Boiss. II, 5:452. 1906, first noted the affinities of Hemsley's species to *Stillingia*, but he did not make a formal transfer. It is difficult to understand why Pax and Hoffmann failed to make the transfer to *Stillingia*, but maintained both *Sapium Bodenbenderi* O. Ktze. and *Sapium subsessile* Hemsl.

I have not seen *Weir* 315 (the specimen at Kew having been temporarily misplaced), and the wide geographic separation of this specimen (collected in the state of São Paulo, Brazil) from those of Bodenbender and Hieronymus (State of Córdoba, Argentina) is hard to explain. This may be a relict species on the old land masses of southern Brazil and in the Sierra de Córdoba, Argentina.

Fig. 6. *Stillingia peruviana*.3. *STILLINGIA peruviana* D. J. Rogers, spec. nov. (T.: Stork & Horton 10918!).

Frutices 2 m. alti, caulibus lignosis saepe ramosis; rami approximati vel fasciculati teretes graciles, cortice parce lenticellato cineraceo-brunneo, succo lacteo. Folia in ramulis perbrevibus congesta aut alternata si singularia petiolata membranacea anguste elliptica vel lanceolata apice baseque acutis, 2.0–3.5 cm. longa, 0.5–0.8 cm. lata, subtiliter serrulata vel crenulata, basi glandulis 2 minutis cyathiformibus vel nullis, nervo medio prominenti venis secundariis in superficie inferiore manifestis, petiolis gracilibus 2–4 mm. longis supra sulcatis. Inflorescentia ca. 2.5 cm. longa constanter fusco-rubra sub cymula pistillata ima pedunculata, regione superiore staminali ab inferiore pistillato in pedunculo non distincte separato, cymulis pistillatis remotis staminalibus congestis, bractee cymularum pistillarum caudato-acuminatae marginibus saepe involutis, bractee cymularum staminalium

late rhombeae mucronulatae, glandibus disciformibus sessilibus simplicibus. Sepala floris pistillati tria 1 mm. longa minusve. Ovarium sessile 3-carpellatum, stylis 3 mm. longis. Cymulae staminales 5- vel 7-florae; floribus subsessilibus ca. 1-2 mm. longis, calyce tenuiter 2-lobato, lobis serrulatis; pollen sphaeroideum foraminibus 3 exosporiis granularibus. Fructus profunde 3-lobatus ca. 5 mm. latus, lobis gynobasis ca. 2 mm. longis; seminibus ellipsoideis vel ovoideis ca. 3 mm. longis 2.5 mm. latis laevibus pallide brunneis, caruncula parva sub micropyllo affixo.

Fairly common in shrubland along rivers at altitudes from 2500 to 2900 m. Fruit said to be edible.

PERU: HUANCVELICA: Prov. Tayacaja, Mantaro Valley, near La Mejorada, rainy green shrubwood, Mar. 21, *Weberbauer 7605* (GH); 4 km. south of Mejorada, Mar. 14, *Stork & Horton 10918* (F, HOLOTYPE).

The nearest relatives of *S. peruviana* occur in the Sierra de Córdoba, Argentina, and in southern Mexico and Central America. In evolutionary sequence, it probably is a connecting link between the more primitive shrubby species of the mountains of southern Brazil and the more advanced shrubs of the mountains of Central America and Mexico.

The distinctive features of this species are its narrowly elliptic to lanceolate leaves, frequently grouped on short side branches, and its deep red, slender inflorescence.

Vernacular name: Cabra-cabra (Peru).

4. *STILLINGIA SANGUINOLENTA* Muell. Arg. in *Linnaea* 32:88. 1863. (T.: *Ehrenberg s. n.*).

Stillingia sanguinolenta α. *lanceolata* Muell. Arg. loc. cit. 1863. (T.: *ibid.*).

Stillingia sanguinolenta β. *angustifolia* Muell. Arg. loc. cit. 1863. (T.: *Schiede?* [*Ehrenberg*] 1245).

Shrubs 1-3 m. tall; stems woody, frequently branched, the branches opposite to approximate, terete, slender, the lenticellate bark roughened, the sap milky. Leaves opposite, widely spaced, petiolate, membranaceous, narrowly to broadly elliptic, 1.7-8.6 cm. long, 1.0-2.6 cm. wide, apex acuminate to acute, base acute, usually with two cyathiform glands, serrulate, the midrib and secondary venation prominent; petiole 0.2-1.0 cm. long. Inflorescence 3.0-6.3 cm. long, shortly pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, widely spaced, not distinctly separate upon the peduncle; bracts of the pistillate and staminate cymules cuspidate, about 1.5-2.0 mm. long, the cyathiform glands sessile. Sepals of the pistillate flower 3, cuneate, serrulate, about 2 mm. long; ovary sessile, 3-carpellate; styles 2-4 mm. long. Staminate cymules 7- to 9-flowered, the flowers subsessile, about 2 mm. long; calyx shallowly 2-lobed, the lobes serrulate; pollen ellipsoid, circular in cross-section, with 3 pores, the exine reticulate to coarsely punctate. Fruit deeply 3-lobed, 6-8 mm. wide, the lobes of the gynobase 3-4 mm. long; seeds ellipsoid, about 4.5-5.0 mm. long, 4 mm. wide, the testa slightly rugulose, the base flattened, the caruncle small.

Fig. 7. *Stillingia sanguinolenta*.Fig. 8. *Stillingia microsperma*.

In deep leaf mold, among rocks, dense oak woods of canyon floor, openly wooded arroyos, on lower slopes, river gravel, hills, and occasionally in desert regions, at altitudes from 500 to 1000 m. Flowers from about the middle of March through June, sometimes to October, and fruits from about the first of June through the last of August.

MEXICO: TAMAULIPAS: Sierra de San Carlos, vic. of San Miguel, *Bartlett* 10570 (F, US); Sierra de San Carlos, vic. of El Milagro, *Bartlett* 11025 (F, GH, US). NUEVO LEON: Municipio de Villa Santiago, *Mueller* 2026 (F, MICH, MO, TEX); Canyon Diente, near Monterrey, *Mueller* 2668 (GH, UC); on Pan American Highway, Monterrey, *Frye & Frye* 2493 (GH, MO, NY, US); Montemorelos, *Nelson* 6695 (GH, US); Sierra Madre, Monterrey, C. H. & H. T. *Mueller* 467 (F, TEX); Guajuco, 27 mi. s. e. of Monterrey, *E. Palmer* 1255 (GH, US); hills near Monterrey, *Pringle* 2070 (F, GH); river gravel near Monterrey, *Pringle* 13756 (GH, MICH, US); river gravel, Monterrey, *Pringle* 2534 (BR, F, GH, MO, NY, UC, US). SAN LUIS POTOSÍ: Guascama, *Purpus* 4980 (F, GH, MO, UC, US); Sierra Tablon, *Purpus* 5464 (F, GH, MO, NY, UC, US); Alvarez, *E. Palmer* 234 (GH, NY, US). HIDALGO: Zimapán, *Kenoyer s. n.* (MICH, MO); foot of Chipique (Hidalgo?), *Kenoyer* 266 (F). CHIAPAS: Comitán, *Goldman* 902 (US). PUEBLA: vic. of San Luis Tultitlanapa, Puebla, near Oaxaca, *Purpus* 3523 (UC). STATE AND LOCALITY UNKNOWN: *Coulter* 1502 (GH); *Pavon s. n.* (D).

The identity of the collector of the type specimen of *S. sanguinolenta* β . *angustifolia* is doubtful. *Mueller* cites "Schiede? 1245", but *Pax* in *Engl. Pflanzenr.* IV, Fam. 147, V:191. 1912, cites *Ehrenberg* 1245, with the same locality as *Mueller*'s. Since this specimen was in the Berlin Herbarium, it is safe to assume that *Pax* cited the correct collector.

Although the specimen cited by *Mueller* for β . *angustifolia* was unavailable, it is evident from his descriptions that the varieties are based on leaf variations. In the material available for this monograph are specimens which show that there is no definite break from the smallest to the largest leaf, and no geographical basis

for separating the varieties from the parent species. In addition, the floral structure is rather stable in all specimens examined, without sufficient evidence for maintaining any subsidiary entities.

5. *STILLINGIA MICROSPERMA* Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:187. 1912. (T.: *Heyde & Lux 4265!*).

Open shrubs 1.0–2.5 m. tall; stems woody, sparsely branched, the branches opposite to fascicled, terete, slender, sparsely lenticellate, the sap milky. Leaves opposite to approximate, widely spaced, petiolate, membranaceous, elliptic, 7.5–12.8 cm. long, 2.3–4.0 cm. wide, apex acuminate to acute, base broadly acute to obtuse, usually with 2 cyathiform glands, finely serrate, the midrib and secondary venation prominent; petiole 0.4–1.1 cm. long, pale green above, paler beneath. Inflorescence 3.0–8.7 cm. long, pedunculate and somewhat thickened below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, not distinctly separate upon the peduncle, the pistillate distant, the staminate overlapping; bracts of pistillate and staminate cymules elliptic, mucronulate, about 1.5 mm. long. Sepals of the pistillate flower 3, elliptic; ovary sessile, 3-carpellate; styles about 2 mm. long. Staminate cymules 7- to 9-flowered, the flowers subsessile, about 1.5 mm. long; calyx deeply 2-lobed, the lobes serrulate; pollen spheroid to ellipsoid, circular in cross-section, with three pores, the exine finely punctate. Fruit about 8 mm. wide, globular, not deeply 3-lobed, the lobes of the gynobase about 4 mm. long; seeds ellipsoid, about 5 mm. long, 4 mm. wide, smooth or slightly rugulose, the micropylar end slightly flattened, the caruncle small.

In open creek beds, oak woods, mountains, at altitudes from 1400 to 3000 m. on south-facing slopes, scrub-oak hillsides. Flowers from July through August, and fruits from August through November, and the first of January. Shrub said to have a disagreeable odor.

BRITISH HONDURAS: El Cayo District, in open creek bed, San Agustín, *Lundell 6740* (C, F, GH, MICH, NY, S, TEX, US).

GUATEMALA: HUEHUETENANGO: along Aguacatan road east of Huehuetenango at km. 13–14, *Standley 82033* (F); Cumbre Papal, on south-facing slopes between Cuilco and Ixmiqui, *Steyermark 50919* (F). JALAPA: La Laguna, at base of Volcan Jumay, 1 mi. north of Jalapa, *Steyermark 32291* (F); mountains along the road between Jalapa and Paraiso, *Standley 77230* (F); no locality, *Ruano 1358* (F). SANTA ROSA: Santa Rosa, *Heyde & Lux 4265* (GH, US).

6. *STILLINGIA diphtherina* D. J. Rogers, spec. nov. (T.: *Williams & Molina 10603!*).

Frutices diffusi 1–2 m. alti, caulibus lignosis saepe ramosis; rami oppositi vel fasciculati teretes graciles rigidi, cortice moderate lenticellato cineraceo saepe nigro. Folia opposita breviter petiolata lanceolata vel anguste elliptica coriacea pallide viridia, odore resinae, 1.8–3.5 cm. longa 0.6–1.8 cm. lata, apice acuto vel rotundato base anguste obtuso, margine crenulato base glandulis 2 cyathiformibus, nervio medio prominenti, venis secundariis obscuris, petiolo 1–2 mm. longo. Inflorescentia 3–5 cm. longa parce flexuosa, pedunculo elongato sub cymula pistillata ima

Fig. 9. *Stillingia diphtberina*.

aliquando crassato, cymulis superioribus staminalibus et cymulis inferioribus pistillatis spiralibus remotis; bracteae late ellipticae mucronulatae integrae, glandibus patelliformibus breviter pedicellatis. Sepala floris pistillati 3 late elliptica ca. 1 mm. longa subtiliter serrulata. Ovarium sessile 3-carpellatum, stylis ignotis. Cymulae staminales 7- vel 9-florae, tenuiter 2-lobatae lobis serrulatis; pollen sphaeroideum, foraminibus 3 exosporiis granularibus. Fructus ignotus. Lobi gynobasis 3-4 mm. longi; semina ellipsoidea vel ovoidea ca. 4 mm. longa 3 mm. lata extremo micropylari parce complanato testa laevi basi rotundata caruncula parva.

In barrancos in pine barrens, rocky limestone slopes at altitudes from 800 to 1400 m. Flowers in July, and fruits from August to the first of October.

GUATEMALA: HUEHUETENANGO: between Nenton and Las Palmas, via Yalisjao, Rincon Chiquite, Chiquial, Guaxacana, in Sierra de los Cuchumatanes, *Steyermark 51648* (F). QUICHE: without locality, *Aguilar 760* (F), *1106* (F).

HONDURAS: MORAZAN: west of Guinope, *Williams & Molina 10603* (F, MO HOLOTYPE, UC); Tanque, *Valerio 860* (F); Zamorano, *Valerio 2158* (F); San Antonio de Oriente, *Valerio 3130* (F, MO).

This species is most closely related to *S. microsperma*, from which it may easily be distinguished by its small, leathery, short-petiolate leaves, the slender open inflorescence, and the stiff terete branches. Although none of the specimens cited have an attached fruit, it is apparent from the fragments contained in packets that the fruit is shallowly 3-lobed.



Fig. 10. *Stillingia diphtherina*.



Fig. 11. *Stillingia bicarpellaris*.

7. *STILLINGIA BICARPELLARIS* S. Wats. in Proc. Am. Acad. 21:455. 1886. (T.: *Pringle 1281*).

Shrubs 1.5–3.0 m. tall; stems woody, profusely branched, the branches alternate to approximate, terete, the bark slightly roughened, sparsely lenticellate, leaf scars prominent. Leaves alternate, closely spaced, shortly petiolate to sessile, membranaceous, lanceolate to linear, 1.7–5.5 cm. long, 0.2–0.8 cm. wide, apex acute, the base acute, with occasional cyathiform glands, irregularly serrulate to entire, the midrib prominent, the secondary venation obscure; petiole about 1 mm. long. Inflorescence 1.5–2.9 cm. long, sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, not distinctly separate upon the peduncle; bracts of pistillate and staminate cymules broadly elliptic, serrulate, mucronulate, the glands cyathiform, sessile. Sepals of pistillate flower 2, rarely 3, broadly cuneate to rhombic, serrulate; ovary sessile, 2-, rarely 3-carpellate; stigmas 2, rarely 3, style and stigma about 2–3 mm. long. Staminate cymules 6- to 7-flowered, the flowers subsessile, about 1 mm. long; calyx

deeply 2-lobed, the lobes entire, mucronulate; pollen nearly spheroid, with 3 segments, 3 pores, the exine granular to reticulate. Fruit slightly 2-, rarely 3-lobed, 6-8 mm. wide, the lobes of the gynobase 3-5 mm. long; seeds nearly spheroid, about 6 mm. long, 5.5 mm. wide, the testa smooth, shiny, the micropylar end very slightly flattened, the base rounded, the caruncle small.

Thick underbrush in woodland associations of pines, oaks, and junipers, in mountains at altitudes up to 3100 m. Flowers and fruits from the last of June through October.

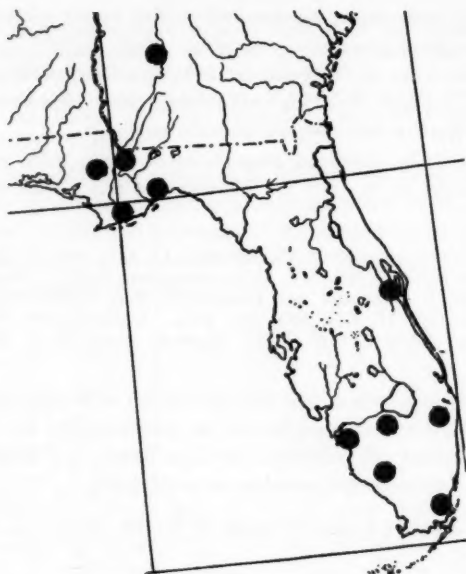
MEXICO: COAHUILA: summit of Mt. Jimulco, 13 kilo. east of Jimulco, *Stanford, Retherford & Northcraft 94* (MO, NY, UC); mountains, Jimulco, *Pringle 128* (A, BR, F, GH HOLOTYPE, NY). HIDALGO: near Ixmiquilpan, *Rose, Painter & Rose 8953* (US); Ixmiquilpan, *Purpus 1454* (F, GH, MO, NY, UC). GUANAJUATO: "sur la montagne près de Guanajuato," *Duges 242* (F, US). PUEBLA: rocky places, Tehuacán, *Purpus 1320* (UC).

If the dimerous structures of the pistillate flowers of *S. bicarpellaris* were constant features, a third subgenus might well be established for this species. Since, however, both dimerous and trimerous pistillate flowers are found on the same plant, I have not considered this procedure to be advisable.

8. *STILLINGIA AQUATICA* Chapm. Fl. South. U. S. 405. 1865. (T.: *Chapman s. n.* lectotype, US!).

Erect shrubs 5.0-11.6 dm. tall. Primary root very short, the secondary filiform, closely set on primary, forming a dense mat. Stems single, terete, tapering gradually from the base, leafless below the branches, the bark lenticellate, light gray to brown, the wood very light, the branches fascicled or dichotomous near the apex of the main axis, the leaf scars prominent on the older branches. Leaves alternate, crowded, mostly confined to the branch apices, petiolate, membranaceous, lanceolate to linear, 3.5-8.5 cm. long, 0.4-1.7 cm. wide, apex acuminate to acute, base narrowly obtuse, without cyathiform glands, irregularly crenulate to serrulate, the midrib prominent, the secondary venation obscure; petiole 0.1-0.6 cm. long. Inflorescence 3.0-3.8 cm. long, sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, distinctly separate upon the peduncle; bracts of pistillate and staminate cymules entire, sharply cuspidate, about 2 mm. long, the crateriform glands shortly pedicellate. Sepals of pistillate flower 3, rounded, slightly crenulate; ovary sessile, 3-carpellate; styles and stigmas about 4 mm. long. Staminate flowers 11-13 in a cymule, subsessile, about 1.0 mm. long; calyx shallowly 2-lobed, the lobes entire; pollen ellipsoid to ovoid, with 3 pores, the exine coarsely punctate. Fruit deeply 3-lobed, 5-6 mm. wide, the lobes of the gynobase 2.5-3.0 mm. long; seeds spheroid, 2-3 mm. in diameter, testa strongly rugose, the flattened micropylar end hippocrepiform, the base rounded, the caruncle small.

In shallow ponds, wet pine barrens, edges of flatwoods ponds, cypress swamps, wet sandy soils, moist ditches, in the Everglades.

Fig. 12. *Stillingia aquatica*.

UNITED STATES: GEORGIA: Sumter Co., FLORIDA: Brevard, Collier, Dade, Franklin, Gadsden, Hendry, Lee, Palm Beach, Wakulla, and Washington counties.

No doubt many of the specimens examined from Florida are of hybrid origin, but since these specimens were not included in my study of the process of introgressive hybridization between *S. aquatica* and *S. sylvatica*, I have not indicated their hybrid nature by annotation of the specimen. The following specimens of my own collection of *S. aquatica* showing introgression with *S. sylvatica* are conserved in the herbarium of the Missouri Botanical Garden:

UNITED STATES: FLORIDA: HENDRY CO.: between LaBelle and Immokalee, in edge of cypress swamp, Rogers 8; near Immokalee, large population, cypress swamp, Rogers 9. COLLIER CO.: 3 mi. se. of Naples, Rogers 10. PALM BEACH CO.: 15 mi. sw. of Lake Worth in small cypress pond, Rogers 14-2, 14-4. MARTIN CO.: 1 mi. s. of Stuart, in cypress pond, Rogers 15-4, 15-8, 15-9. (See also specimen citations of *S. sylvatica* sp. *sylvatica*, p. 241).

Vernacular name: Corkwood.

Series 2. DICHOTOMAE D. J. Rogers, ser. nov.

§ *Pachycladae* Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:186. 1912.

Frutices; caules plerumque succulenti; folia succulenta; pollen ellipsoideum, foramine uno laterali. Braziliae orientali.

KEY TO THE SPECIES

- A. Stems woody, leaves crowded, spiral, with 2 cyathiform glands at the base; staminate cymules 7- to 9-flowered..... 9. *S. Uleana*
 AA. Stems succulent; leaves widely spaced, or whorled when closely set,

without glands, or the glands scutelliform at base of leaf; staminate cymules 3- to 7-flowered.

- B. Branches alternate or fascicled; leaves long-petiolate, mostly alternate, trapezoid..... 10. *S. trapezoides*
 BB. Branches opposite; leaves short-petiolate, opposite or verticillate, narrowly to broadly elliptic or spatulate.
 C. Stems enlarged at the nodes, opaque; leaves broadly elliptic, without glands; sepals distinct..... 11. *S. dichotoma*
 CC. Stems not enlarged at the nodes, vernicose; leaves narrowly elliptic to spatulate, with 2 basal scutelliform glands; sepals united into a truncate annulus..... 12. *S. saxatilis*

9. *STILLINGIA ULEANA* Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:187. 1912. (T.: *Ule* 7135!).

Shrubs 2-6 m. tall; stems woody, branches infrequent, fascicled, slender, terete, sparsely lenticellate, opaque, gray-brown, frequently blackened. Leaves alternate, crowded, petiolate, succulent, elliptic to spatulate, 4-5 cm. long, 1.2-1.5 cm. broad, apex acute, base narrowly acute, crenulate, with 2 basal scutelliform glands and infrequent, irregularly spaced elongate-crateriform glands toward the tips, the midrib prominent, the secondary venation sunk in the fleshy tissue; petiole about 0.3-0.5 cm. long. Inflorescence 5-7 cm. long, slightly flexuose, pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate regions distinctly separate upon the peduncle, the cymules spiral, crowded, bracts of pistillate cymule unknown, the staminate broadly cuneate to rhombic, entire, the glands elliptic, flattened, tightly clasping the peduncle. Sepals of pistillate flower unknown; ovary sessile, 3-carpellate; styles unknown. Staminate cymules 7- to 9-flowered, the flowers subsessile, about 2-3 mm. long; calyx shallowly 2-lobed, the lobes entire; pollen grains ellipsoid, with 1 pore, the exine coarsely reticulate. Lobes of the gynobase about 3 mm. long. Fruit and seed not seen.

BRAZIL: BAHIA: Sincorá, Serra de Vendinha, 800 m., *Ule* 7135 (K, photos in F, GH, MO, US).

10. *STILLINGIA TRAPEZOIDEA* Ule, in Engl. Bot. Jahrb. 42:233. 1908. (T.: *Ule* 7160!).

Shrubs 1-4 m. tall; stems succulent, angular, infrequently branched, the branches alternate or fascicled, slender, sparsely lenticellate, light gray- to reddish-brown. Leaves alternate, scattered, or crowded near insertion of inflorescence, petiolate, succulent, elliptic-trapezoid, 3-4 cm. long, 1-2 cm. broad, apex abruptly acuminate, base narrowly acute, without cyathiform glands, crenulate, the midrib and secondary venation immersed in the fleshy tissue; petiole 0.5-1.0 cm. long. Inflorescence 1.2-2.0 cm. long, slender, pedunculate below the lowest pistillate cymule, the cymules spiral; bracts of the pistillate cymules broadly elliptic, mucronulate, concave, the staminate broadly caudate-acuminate; the glands elliptic, convex. Sepals of pistillate flower 3, broadly elliptic to obovate, serrulate; ovary sessile, 3-carpellate; styles 2-3 mm. long. Staminate cymules 3- to 5-flowered, the flowers subsessile; calyx 2-lobed. Fruit about 7 mm. broad, deeply 3-lobed. Seed not seen.

Details of the staminate flower have been taken from the descriptions given by Ule and Pax & Hoffmann. The specimen from Kew had no mature staminate flowers.

BRAZIL: PIAUHY: in der *catinga*²² in der Serra Branca, Jan., 1907, Ule 7160 (K, photos in F, GH, MO, US).

11. *STILLINGIA DICHOTOMA* Muell. Arg. in *Linnaea* 32:88. 1863. (T.: Riedel 185!).

Shrubs to 1 m. tall; stems succulent, thickened, enlarged at the nodes, leaf scars prominent, branches opposite, without lenticels, opaque, gray- to reddish-brown, frequently blackened. Leaves verticillate, succulent, petiolate, broadly elliptic, 5–12 cm. long, 3–5 cm. broad, apex acute to shortly acuminate, base broadly acute, without cyathiform glands, serrulate to crenulate, the midrib prominent, the secondary veins obscure; petiole 0.5–1.5 cm. long. Inflorescence 4–8 cm. long, slightly flexuose, pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate regions distinctly separate upon the peduncle, the cymules widely spaced, spiral; bracts of pistillate and staminate cymules concave, obovate, truncate, mucronulate; the glands patelliform, somewhat auriculate. Sepals of pistillate flowers 3, about 2 mm. long; ovary pedicellate, exerted beyond the bract and sepals, 3-carpellate; styles about 3 mm. long. Staminate cymules 10- to 12-flowered, the flowers subsessile, about 1.5–2.0 mm. long; calyx shallowly 2-lobed, the lobes serrulate; pollen ellipsoid, triangular in cross-section, with 1 lateral pore, the exine finely to coarsely punctate. Fruit deeply 3-lobed; lobes of the gynobase about 3 mm. long; seeds ovoid to slightly ellipsoid, about 4 mm. long, 3.5 mm. wide, tuberculate-striate, gray-brown, the caruncle small.

BRAZIL: RIO DE JANEIRO: Forterepe du Pic de Sta. Crus près de Rio de Janeiro, *Glazion* 6126 (C, G, S); in montosis saxosis prope Rio de Janeiro, *Riedel* 185 (C, F, G HOLOTYPE, GH, NY).

12. *STILLINGIA SAXATILIS* Muell. Arg. in *Mart. Fl. Bras.* 11²:539. 1874. (T.: Riedel 1172!).

Gymnostillingia loranthacea Muell. Arg. in *Mart. Fl. Bras.* 11²:541. 1874. (T.: Blanchet 271!).

Stillingia loranthacea (Muell. Arg.) Pax & Hoffm. in *Engl. Pflanzenr.* IV. Fam. 147. V:185. 1912.

Shrubs to 1.2 m. tall; stems succulent, infrequently branched, the branches opposite, thickened, leaf scars prominent, without lenticels, vernicose, red-brown to frequently blackened. Leaves alternate, crowded, sessile to petiolate, somewhat succulent, elliptic to spatulate or oblanceolate, 3–6 cm. long, 0.8–2.3 cm. broad, apex acute to acuminate, base narrowly acute with 2 suborbicular inset glands, irregularly serrulate to serrate, with frequent irregularly spaced scutelliform glands toward the tip, the midrib prominent, secondary venation immersed in the fleshy

²²"Catinga" refers to a region of open scrub forest, with mostly deciduous species and very low rainfall.

tissue; sessile or the petiole 0.1–0.8 cm. long. Inflorescence 2.5–6.4 cm. long, slightly flexuose, pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate regions distinctly separate upon the peduncle, the cymules widely spaced, spiral; bracts of pistillate and staminate cymules concave, obovate, truncate, mucronulate, the glands flattened, auriculate. Sepals of pistillate flower united into a truncate annulus, or greatly reduced; ovary subsessile, 3-carpellate; styles about 3 mm. long. Staminate cymules 5- to 7-flowered, the flowers subsessile, about 1.5 mm. long; calyx very shallowly 2-lobed, the lobes unevenly serrulate; pollen ellipsoid, with one lateral pore, the exine granular. Fruit deeply 3-lobed; lobes of the gynobase 3–4 mm. long; seeds ellipsoid, about 3.5 mm. long, 2.5 mm. wide, smooth, brown, the caruncle small.

In rocky, hilly areas. Flowers and fruits from October through January.

BRAZIL: BAHIA: *Blanchet 271* (G, photos F, MO); Serra das Almas, 1700 m., *Luetzelburg 172* (NY). MINAS GERAIS: Serra da Lapa, *Riedel 1172* (G, photos F, MO); Municipio Diamantina, Bom Sucesso, *Barreto 9675* (F). WITHOUT LOCALITY: *Glaziov 19852* (C).

The only known specimen of *S. loranthacea*, *Blanchet 271*, is a mere fragment on which no pistillate flowers are present. However, the great similarity of vegetative and floral characters, including the morphology of the pollen grain, leads me to the conclusion that the *Blanchet* specimen is but a variant of the species *S. saxatilis*.

Series 3. SYLVATICAE (Pax & Hoffm.) D. J. Rogers, stat. nov.

§ *Sylvaticae* Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:191. 1912.

Subshrubs arising from a woody underground base; stems herbaceous or subherbaceous, green to reddish-brown, without lenticels.

KEY TO THE SPECIES AND SUBSPECIES

- A. Glands of the subtending bracts of the cymules elongate, tubiform or urceolate; leaf margins with a broad callus; Paraguay, Argentina and Bolivia.
 - B. Leaves generally narrowly elliptic to linear, without glands at base of the blade; pistillate bracts broadly rhombic; caruncle hippocrepiiform, attached below the micropyle..... 13. *S. salpingadenia*
 - BB. Leaves generally elliptic to broadly elliptic, with 2 scutelliform or cyathiform glands at base of the blade; pistillate bracts elliptic to obovate; caruncle rhombic, surrounding the micropyle..... 14. *S. scutellifera*
- AA. Glands of the subtending bracts of the cymules flattened, disciform, patelliform or cyathiform; leaf margins with a narrow callus or only the serrulations callose; Brazil, Mexico, Central and North America.
 - C. Inflorescence pedunculate below the lowest pistillate cymule; leaves usually with 2 or more cyathiform glands at base of blade, narrowly callose, serrulate; Brazil, Central America and Mexico.
 - D. Leaves sessile, usually 2 cm. long or less; staminate cymules 10- to 12-flowered, the flowers pedicellate; Brazil..... 15. *S. Dusenii*
 - DD. Leaves petiolate, usually 3 cm. long or longer; staminate cymules 3- to 5-flowered, the flowers subsessile; Mexico and Central America..... 16. *S. zelayensis*
 - CC. Inflorescence sessile below the lowest pistillate cymule; leaves without glands at base of the blade; United States and extreme northeastern Mexico.

- E. Leaves linear; seeds truncate at base; secondary roots fibri-
form; southern Oklahoma, through central Texas to north-
eastern Mexico, in limestone soils..... 17. *S. texana*
- EE. Leaves elliptic, or spatulate to obovate (except ssp. *tenuis*,
with very narrowly elliptic to linear leaves); seeds rounded
at the base; secondary roots fusiform; southern Virginia to
Florida to Texas and New Mexico, mostly on sands..... 18. *S. sylvatica*
- F. Leaves elliptic, spatulate or obovate; southern Virginia
to Florida to Texas and New Mexico, exclusive of extreme
southeastern Florida, in sands..... 18a. *S. sylvatica*
ssp. *sylvatica*
- FF. Leaves very narrowly elliptic to linear; extreme south-
eastern Florida, on limestone outcrops..... 18b. *S. sylvatica*
ssp. *tenuis*

13. *STILLINGIA SALPINGADENIA* (Muell. Arg.) Huber, in Bull. Herb. Boiss. II,
6:452. 1906.

- Sapium salpingadenium* Muell. Arg. in Linnaea 32:121. 1863. (T.: D'Orbigny 918!).
Excoecaria salpingadenia (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1209. 1866.
Sapium haematospermum sensu Chodat, in Bull. Herb. Boiss. II, 1:399. 1901, non Muell.
Arg. in Linnaea 34:217. 1865.
Sapium cupuliferum Hemsl. in Hook. Icon. Pl. 28:t. 2679. 1901. (T.: Hagenbeck s. n.).
Sapium salpingadenium Muell. Arg. var. *salicina* Chodat & Hassler, in Bull. Herb. Boiss.
II, 5:677. 1905. (T.: Hassler 6346!).
Stillingia salpingadenia (Muell. Arg.) Huber, ssp. *anadena* Pax & Hoffm. in Engl. Pflanzenz.
IV. Fam. 147. V:190. 1912. (No type cited).
Stillingia salpingadenia ssp. *anadena* var. *δ. cupulifera* (Hemsl.) Pax & Hoffm. loc. cit.
1912.
Stillingia salpingadenia ssp. *anadena* var. *ε. salicina* (Chodat & Hassler) Pax & Hoffm. loc.
cit. 1912.

Subshrubs 3–10 dm. tall; stems subherbaceous, woody toward the base, in-
frequently branched, the branches alternate to approximate, leaf scars on older
parts prominent, sparsely lenticellate to elenticellate, reddish- to gray-brown.
Leaves alternate to approximate, subsessile to petiolate, membranaceous, narrowly
elliptic to slightly lanceolate, 4–7 cm. long, 0.8–2.5 cm. broad, apex acuminate,
mucronulate, base acute, without cyathiform or scutelliform glands, the margin
serrulate, broadly callose, the midrib prominent, secondary venation obvious, not
prominent; petiole 0.1–0.4 cm. long. Inflorescence 3.5–8.5 cm. long, sessile or
shortly pedunculate below the lowest pistillate cymule, the upper staminate and
lower pistillate cymules spiral, not distinctly separate upon the peduncle, the pistil-
late cymules widely spaced, the staminate crowded; bracts of pistillate and stam-
inate cymules broadly rhombic, mucronulate, the glands tubiform to urceolate,
about 2.5 mm. long. Sepals of pistillate flower 3, elliptic, mucronulate; ovary
sessile, 3-carpellate; styles about 4–5 mm. long. Staminate cymules 7- to 9-
flowered, the flowers subsessile, about 2 mm. long; calyx shallowly 2-lobed, the
lobes entire to slightly serrulate; pollen ovoid to ellipsoid, with 3 pores, the exine
unevenly striate to granular. Fruit not seen. Lobes of the gynobase 3–4 mm.
long; seeds ellipsoid, 6 mm. long, 4.5 mm. wide, slightly rugulose, light gray, the
caruncle small, hippocrepiform, attached below the micropyle.

In rocky areas, hill regions, high plains above flowing rivers, generally below 1000 m. alt. Flowers from September through December and fruits from October through February.

BOLIVIA: SANTA CRUZ: Chiquitos, D'Orbigny 918 (F, P, photos F, US).

PARAGUAY: Cordillera de Altos, Fiebrig 99b (A, F, G, GH, LIL), same locality, Hassler 2110 (G) (fasciated), Hassler 3394 (A, F, G); Fort Lopez, Hassler 888 (G); Cerros de Tobaty, Hassler 6346 (A, F, G, K); in regione cursus superioris fluminis Apa, Hassler 7782 (G).

14. *STILLINGIA scutellifera* D. J. Rogers, nom. nov.

Stillingia saxatilis sensu Chodat & Hassler, in Bull. Herb. Boiss. II, 5:676. 1905, non Muell. Arg. in Mart. Fl. Bras. 11²:539. 1874.

Stillingia saxatilis var. *salicifolia* Chodat & Hassler, loc. cit. 1905. (T.: Hassler 4360!), non *S. salicifolia* (Torr.) Raf.

Stillingia saxatilis var. *salicifolia* f. *latior* Chodat & Hassler, loc. cit. 1905. (T.: *ibid.*).

Stillingia saxatilis var. *salicifolia* f. *angustior* Chodat & Hassler, loc. cit. 1905. (T.: Hassler 4424).

Stillingia saxatilis var. *grandifolia* Chodat & Hassler, loc. cit. 1905. (T.: Hassler 4794!).

Stillingia salpingadenia (Muell. Arg.) Huber ssp. *saxatilis* (Chodat & Hassler) Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:189. 1912.

Stillingia salpingadenia ssp. *saxatilis* var. *a. elliptica* Pax & Hoffm. loc. cit. 1912. (T.: Hassler 6790!).

Stillingia salpingadenia ssp. *saxatilis* var. *β. grandifolia* (Chodat & Hassler) Pax & Hoffm., loc. cit. 190. 1912.

Stillingia salpingadenia ssp. *saxatilis* var. *γ. angustior* (Chodat & Hassler) Pax & Hoffm., loc. cit. 1912.

Subshrubs 3–7 dm. tall; stems herbaceous, arising from a perennial, woody underground base, single or several together, unbranched, or, if branched, the branches alternate to fascicled, leafy to the base, without lenticels, red-brown. Leaves alternate to approximate, subsessile to shortly petiolate, stiffly membranaceous, broadly to narrowly elliptic, 3–8 cm. long, 1–3 cm. broad, apex acute, mucronulate, base acute, with 2 scutelliform or cyathiform glands, the margin serrulate, broadly callose, the midrib and secondary venation prominent; petiole 0.1–0.7 cm. long. Inflorescence 2.8–11.8 cm. long, sessile to shortly pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules relatively widely spaced, the staminate crowded, bracts of pistillate and staminate cymules elliptic to broadly rhombic, serrulate, sharply mucronulate, the glands infundibuliform, 2–3 mm. long. Sepals of pistillate flower 3, rhombic, serrulate, bluntly mucronulate; ovary subsessile, 3-carpellate; styles about 3–5 mm. long. Staminate cymules 3- to 5-flowered, the flowers shortly pedicellate, about 3 mm. long; calyx deeply 2-lobed, the lobes serrulate; pollen spheroid with 3 pores, the exine granular. Fruit not seen. Lobes of the gynobase 4–5 mm. long; seeds ovoid to slightly ellipsoid, about 5 mm. long, 5 mm. wide, slightly rugulose to smooth, dark gray, the caruncle large, waxy, rhombic, surrounding the micropyle.

Grassy campos, near margins of forest, high campos, in river regions at altitudes usually below 500 m., but occasionally to 1000 m. Flowers from October to February and fruits from November through March.

ARGENTINA: MISIONES: Dept. Cainqua, Campo Grande, *Pierotti* 5365 (LIL), 5384 (LIL); Dept. Candelaria, Santa Ana, *Schwarz* 3520 (LIL); Dept. San Ignacio, El Destierrro, *Schwarz* 1354 (LIL); Zob. Roca, *Schwarz* 5195 (LIL); Santa Maria, *Schwarz* 2518 (LIL); Mariá Antonia, *Schwarz* 8391 (LIL); Posadas, *Ekman* 506 (S, US).

PARAGUAY: Pirayu, *Balansa* 1708 (K); Gtangu, près de Villa-Rica, dans les prairies, *Balansa* 1711 (G); Cordillera de Altos, *Fiebrig* 99a (A); Dept. Piribebuy, Colonia Pedro P. Caballero, *Rojas* 1956? (LIL); Villa Rica, *Jørgensen* 3985 (A, C, F, LIL, MO, S, US); Sierra de Maracayu, in regione fluminis Tapiraguay, *Hassler* 4360 (F, GH, S); in regione fluminis Capibary, *Hassler* 4446 (G, S); in regione fluminis Corrientes, *Hassler* 4494 (G); in regione vicine "Igatimi", *Hassler* 4794 (G), 5612 (G); Cordillera Centralis, in regione cursus superioris fluminis Y-aca, *Hassler* 6790 (G); in campo montano pro. Chulola (Chulolo), *Hassler* 6790 (G); auf nasse Stellen, Arecipe, Rio Apa, *Anisits* 2435 (S).

There is little doubt in my mind that *S. scutellifera* is sufficiently distinct from *S. salpingadenia* to be considered as a separate species. It is apparent, however, that rather free hybridization is taking place between the two species, with the result of confusion when an effort is made to key some of the individuals of either species.

15. *STILLINGIA DUSENII* Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, XVII:202. 1924. (T.: *Dusen* 10440!).

Subshrubs 1-3 dm. tall; stems herbaceous, arising from a perennial, woody, underground base, single or several together, unbranched, or, if branched, the branches alternate to fascicled, leafy to the base, without lenticels, red-brown. Leaves alternate to approximate, widely to closely set, sessile, membranaceous, ovate to elliptic, 1.0-2.5 cm. long, 0.5-1.3 cm. broad, apex acute to rounded, base obtuse to broadly acute, with 2 cyathiform to patelliform glands, the margin serrulate, narrowly callose, the midrib prominent, the secondary venation obscure. Inflorescence 8-12 cm. long, pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate regions spiral, distinctly separate upon the peduncle, the cymules relatively widely spaced; bracts of the pistillate cymules foliaceous, linear, about 5 mm. long, acute, the base auriculate, serrulate, the staminate squamaceous, ovate to broadly elliptic, serrulate, mucronulate, the glands circular, flattened. Sepals of pistillate flower 3, broadly triangular, serrulate, without mucro; ovary sessile, 3-carpellate; styles unknown. Staminate cymules 10- to 12-flowered, the flowers pedicellate, the pedicels about 2 mm. long; calyx shallowly 2-lobed, the lobes serrulate; pollen irregularly spheroid, with 3 pores, the exine granular to coarsely punctate. Mature fruit and seed not seen.

BRAZIL: PARANA: Jaguarihyva, in campo, Oct. 25, *Dusen* 10440 (MO, S); Villa Velha, Jan. 25, *Dusen* 9143 (S); in campo limpo, Oct. 11, *Dusen* 13179 (G, GH, S); in campo, 740 m., *Jonsson* 294a (A).

16. *STILLINGIA ZELAYENSIS* (HBK.) Muell. Arg. in Linnaea 32:87. 1863.

Sapium zelayense HBK. Nov. Gen. et Spec. 2:51. 1817. (T.: *Humboldt & Bonpland* s. n.).

Erect to spreading subshrubs 5-15 dm. tall; stems subherbaceous, arising from a perennial, woody, underground base, terete, older parts hollow, woody, the secondary branches opposite or fascicled, solid or with a small pith, without lenticels,

green- to reddish-brown. Leaves petiolate, membranaceous, elliptic to oblanceolate to spatulate, 2.8–12.5 cm. long, 1.2–4.0 cm. wide, apex acute to acuminate, base acute, usually with 2 cyathiform glands, the margin serrulate, narrowly callose, the midrib and secondary venation prominent; petiole 1–9 mm. long. Inflorescence 5.0–16.0 cm. long, pedunculate and somewhat thickened below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, distinctly separate upon the peduncle, the pistillate cymules distant, the staminate crowded; bracts of the pistillate and staminate cymules broadly elliptic, mucronulate, serrulate, the glands patelliform, sessile. Sepals of pistillate flower 3, narrowly elliptic, about 3 mm. long, mucronulate, serrulate; ovary sessile, 3-carpellate; styles about 3 mm. long. Staminate cymules 3- to 5-flowered, the flowers sessile, about 3 mm. long; calyx deeply 2-lobed, the lobes serrulate; pollen spheroid, with 3 pores, the exine reticulate. Fruits shallowly 3-lobed, 0.6–1.8 cm. wide, the lobes of the gynobase 3–9 mm. long; seeds nearly spheroid, about 5.5–6.5 mm. long, 5.5–7.0 mm. wide, testa smooth, shiny, flattened at the micropylar end, the basal end rounded to slightly flattened, the caruncle small.

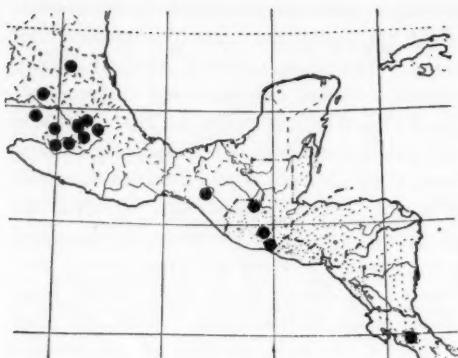
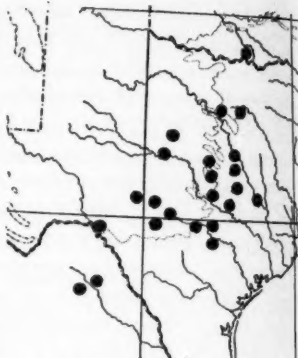
Pine woods and barrancas, rocky hills, shady open slopes on edges of cultivated areas, from about 1200 to 2800 m. altitude. Flowering mostly from about the last of March through the last of August, but occasionally in January and in October, and fruiting from June through October and occasionally in January.

MEXICO: CHIAPAS: Hacienda Monserrate, *Purpus* 9174 (F, GH, MO, NY, UC, US), 9323 (UC); without locality, *Purpus* s. n. (US); pine and oak forest, Fenix (Chiapas?), *Purpus* 10334 (NY). DISTRITO FEDERAL: east of Transfiguración, Russell & Souviron 205 (US). JALISCO: Santa Cruz, M. E. Jones 22 (MO, US); Rio Blanco, E. Palmer 73 (NY, US); near Guadalajara, Pringle s. n. (C, F, LIL). MEXICO: Dist. Temascaltepec, Penon, Hinton 4409 (GH); Dist. Temascaltepec, Temascaltepec, Hinton 1127 (F, GH, NY, US). MORELOS: rocky hill near El Mirador, road from Cuernavaca to Mexico, Williams 3814 (GH); Valle del Tepeite, Lyonnet 988 (US); barranco near Cuernavaca, Pringle 7244 (GH); pine woods about Cuernavaca, Pringle 6886 (BR, F, GH, MO, NY, UC, US). MICHOACAN: vic. of Morelia, Arsène 6679 (MO, US); vic. of Morelia, Arsène 5236 (GH, MO, US); Tancitaro region, above Acahuaato, Munic. Apatzingan, Leavenworth & Hoogstraal 1821 (F, GH); hills near Tepitenga, between Toluca and Morelia, Gregg 727 (MO). PUEBLA: Cerro Tepoxuchil, près Puebla, Nicolas s. n. (LIL, NY); vic. of Puebla, Cerro Tepoxuchil, Arsène 1400 (GH, MO, US); Rancho Losada, vic. of Puebla, Arsène & Nicolas 282 (F). SAN LUIS POTOSÍ: 22° n. lat., alt. 6000–8000 ft., Parry & Palmer 823 (GH, MO, US). TLAXCALA: Huamantla, alt. 8500 ft., Balls B.5640 (A). STATE AND LOCALITY UNKNOWN: Pavon s. n. (G, photos in F, GH).

GUATEMALA: GUATEMALA: without locality, Aguilar 93 (F). QUICHE: without locality, Aguilar 1314 (F). SANTA ROSA: Zamorora, Heyde & Lux 4579 (US); without locality, Deam 6074 (F, GH, MICH, MO, NY, US).

PANAMÁ: CHIRIQUÍ: Boquete Distr., savannah, alt. 4000 ft., Davidson 750 (A, P, MO, US).

The type specimen of *Stillingia zelayensis*, collected by Humboldt & Bonpland, was labelled for locality "prope Zelaya". The actual locality is Celaya, Guanajuato, Mexico.

Fig. 13. *Stillingia zelayensis*.Fig. 14. *Stillingia texana*.17. *STILLINGIA TEXANA* I. M. Johnston, in Contr. Gray Herb. n. s. 68:91. 1923.

Sapium sylvaticum var. *linearifolium* Torr. in Emory, Rept. U. S. & Mex. Bound. Surv. 2:201. 1859. (T.: Schott s. n.!).

Stillingia sylvatica ♂. *linearifolia* (Torr.) Muell. Arg. in DC. Prodr. 15²:1158. 1866.

Stillingia angustifolia (Muell. Arg.) Engelm. ex S. Wats. in Proc. Am. Acad. 18:154. 1883, as to specimen cited, not as to basynym.

Stillingia linearifolia (Torr.) Small, Fl. S. E. United States, 704. 1903; not S. Wats. in Proc. Am. Acad. 14:297. 1879.

Stillingia texana var. *typica* Waterfall, in Rhodora 50:95. 1948.

Stillingia texana var. *latifolia* Waterfall, loc. cit. 1948. (T.: Waterfall 6523!).

Loose erect subshrubs, 2.5–6.0 dm. tall; roots fibriform; stems herbaceous, arising from an enlarged woody root crown, terete or slightly striate, unbranched, or, if branched, the branches fascicled near the apex of the main axis, without lenticels, light green or brown. Leaves alternate, sessile, membranaceous, linear to slightly lanceolate, 1–7 cm. long, 0.3–1.0 cm. wide, apex acute, base narrowly obtuse, without cyathiform glands, serrulate to crenulate, the midrib prominent, slightly decurrent. Inflorescence 3.0–8.0 cm. long, sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, not distinctly separated on the peduncle; bracts of pistillate and staminate cymules narrowly elliptic, mucronulate, sharply denticulate, the patelliform glands sessile. Sepals of pistillate flower 3, elliptic, serrulate; ovary sessile, 3-carpellate; styles about 3 mm. long. Staminate cymules 3- to 5-flowered, the flowers subsessile, about 2.5 mm. long; calyx deeply 2-lobed, the lobes slightly serrulate; pollen mostly spheroid, with 3 pores, the exine granular to reticulate. Fruits shallowly 3-lobed, 4–6 mm. wide, the lobes of the gynobase 2–3 mm. long; seeds mostly ellipsoid, 3–5 mm. long, 2.5–4.0 mm. wide, testa slightly rugulose, with a very slight depression at the micropylar end, the base truncate, the caruncle small.

On limestone soils, mostly in open prairie lands, occasionally on loamy black soils, in rolling country. Flowers from about the last of April through the middle of July, and fruits from the first of June through September.

UNITED STATES: OKLAHOMA: Murray Co. TEXAS: Bell, Bexar, Bosque, Burnet, Comal, Conche, Erath, Fort Bend, Gillespie, Hays, Kendal, Kerr, Lampasas, Mills, Nolan; Parker, Real, Schackelford, Tarrant, Taylor, Travis, Washington, Williamson, Wilson, and Valverde counties.

MEXICO: COAHUILA: Munic. de Muzquiz, near Puerto Santa Ana, Wynd & Mueller 225 (GH, MO, NY, US); Hacienda San Rafael, along the Sabinas River, Wynd 705 (MO, NY, US); Muzquiz, *Marsh 80* (F, TEX); Muzquiz, Yerda Spring, *Marsh 291* (TEX).

One specimen was collected by C. Wright in New Mexico, without locality.

Although Watson gave a description for *S. angustifolia* Engelm., he placed *S. sylvatica* var. *angustifolia* in synonymy. It seems best to follow Johnston's interpretation (in Contr. Gray Herb. n. s. 68:91. 1923), that Watson was making a new combination and the name must apply to the Florida plant (Mueller's type) not, as was done for many years, to the Texan plant. Since no other name was available, Johnston renamed the species, basing it upon var. *linearifolia* Torr.

18. *STILLINGIA SYLVATICA* Garden, ex L. Mant. 19. 1767. (T.: *Garden s. n.*).

Erect or semi-erect subshrubs 2–12 dm. tall; roots fusiform; stems herbaceous to subherbaceous, arising singly or several together from a woody rhizome, terete, unbranched, or, if branched, the secondary branches dichotomous, approximate or fascicled near the apex of the main axis, without lenticels, bark of older parts frequently with transverse and longitudinal cracks, red to reddish-brown or mottled gray and reddish-brown. Leaves alternate, sessile or petiolate, membranaceous, green or sometimes bright red, narrowly elliptic, elliptic, obovate, spathulate or oblanceolate, 2–12 cm. long, 0.3–4.8 cm. wide, apex acute, rounded or emarginate, base narrowly acute to narrowly obtuse, without cyathiform glands, serrulate to crenulate, the midrib prominent, secondary venation obscure; petiole when present 0.1–0.8 cm. long. Inflorescence 2.5–13.0 cm. long, slender or stout, sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, not distinctly separate upon the peduncle; bracts of the pistillate cymule caudate-acuminate to broadly elliptic, serrulate, mucronulate, the staminate broadly elliptic, mucronulate, the glands patelliform or cyathiform, sessile; peduncle and bracts red or yellow-green. Sepals of pistillate flower 3, elliptic, slightly cuspidate, serrulate, 2–3 mm. long; ovary sessile, 3-carpellate; styles about 2–5 mm. long. Staminate cymules 5- to 13-flowered, the flowers subsessile, about 1.5–2 mm. long; calyx shallowly 2-lobed, the lobes entire to slightly serrulate; pollen ellipsoid to spheroid, with 3 pores, the exine reticulate to granular. Fruit shallowly 3-lobed, 0.6–1.2 cm. wide, the lobes of the gynobase 3–6 mm. long; seed ellipsoid 4–8 mm. long, 3–7 mm. wide, testa rugose, the micropylar end flattened, the base rounded, mottled dark gray, the caruncle large, waxy.

18a. *STILLINGIA SYLVATICA* Garden ssp. *SYLVATICA*.

Stillingia sylvatica var. *salicifolia* Torr. in Ann. Lyc. N. Y. 2:245. 1826. (T.: *James s. n.*).

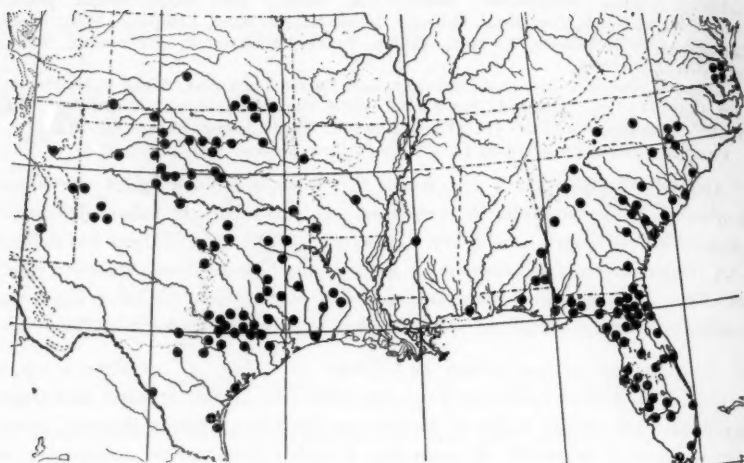
Stillingia salicifolia (Torr.) Raf. in Atl. Jour. 1:146. 1832.

Stillingia lanceolata Nutt. in Trans. Am. Phil. Soc. n. s. 5:176. 1837, (T.: *Pitcher s. n.*).

Stillingia sylvatica a. *spatulata* Muell. Arg. in DC. Prodr. 15:1158. 1866. (T.: *Bosc s. n.*).

Stillingia sylvatica β. *genuina* Muell. Arg. loc. cit. 1866.

Stillingia sylvatica γ. *angustifolia* Muell. Arg. loc. cit. 1866. (T.: *Mitchell s. n.*).

Fig. 15. *Stillingia sylvatica*.

Stillingia angustifolia (Muell. Arg.) Engelm. ex S. Wats. in Proc. Am. Acad. 18:154, 1883, as to basonym, not as to specimen cited.

Stillingia spatulata (Muell. Arg.) Small, Fl. S. E. United States, 704. 1903.

Stillingia salicifolia Small, loc. cit. 1903 (no type cited), non *S. salicifolia* (Torr.) Raf.

Stillingia Smallii Wootton & Standley, in Contr. U. S. Nat. Herb. 19:405. 1915. (Based on the preceding).

Leaves elliptic, spatulate or obovate, 3.2–11.5 cm. long, 0.3–4.8 cm. wide, apex acute, rounded or emarginate. Bracts of the pistillate cymule elliptic.

Coastal plain, except extreme southeastern Florida, well-drained sands, in open pine woods and sometimes on limestone, occasionally on roadsides and railroad banks. Flowers from March through June and fruits from April through September.

UNITED STATES: VIRGINIA: Isle of Wight, Nansemond, Sussex, and Southampton counties. NORTH CAROLINA: Buncombe, Harnett, Iredell, Moore, Richmond, and Scotland counties. SOUTH CAROLINA: Aiken, Beaufort, Berkeley, Charleston, Clarendon, Georgetown, Hampton, Horry, and Lancaster counties. GEORGIA: Bullock, Columbia, Gwinnett, Habersham, Jasper, Macon, Meriwether, Richmond, and Wayne counties. FLORIDA: Alachua, Baker, Bradford, Brevard, Broward, Charlotte, Citrus, Clay, Columbia, Dade, DeSoto, Dixie, Duval, Flagler, Gadsden, Gilchrist, Hardee, Hendry, Hernando, Highlands, Hillsborough, Jefferson, Lafayette, Lake, Lee, Leon, Levy, Liberty, Manatee, Marion, Monroe, Nassau, Orange, Palm Beach, Pasco, Pinellas, Polk, Putnam, St. John's, Sumter, Suwanee, Walton, Wakulla, Union, and Volusia counties. ALABAMA: Dale, Henry, Lee, and Mobile counties. LOUISIANA: Natchitoches, and Rapides parishes. MISSISSIPPI: Holmes Co. TEXAS: Anderson, Angelina, Aransas, Austin, Bailey, Bastrop, Bexar, Brazos, Caldwell, Childress, Dallas, Denton, DeWitt, Dimmit, Erath, Fayette, Fort Bend, Goliad, Gonzales, Gregg, Guadalupe, Hardin, Hemphill, Houston, Hutchinson, Jackson, Jefferson, Kendall, Kenedy, Lamb, Lee, Leon, Lubbock, Medina, Montgomery, Nacogdoches, Newton, Nueces, Parker, Tarrant, Terry, Travis, Upshur, Walker, Waller, Washington, Wichita, Wilson,

and Wood counties. ARKANSAS: Crawford, Jefferson, and Miller counties. KANSAS: Cowley, Harper, Montgomery, Morton, Sedgwick, and Stafford counties. OKLAHOMA: Beaver, Beckham, Blaine, Caddo, Comanche, Cleveland, Ellis, Greer, Kingfisher, Kiowa, Logan, McClain, McCurtain, Muskogee, Oklahoma, Osage, Payne, and Roger Mills counties. NEW MEXICO: Chaves, Harding, and Roosevelt counties.

The taxonomic confusion concerning *S. sylvatica* has resulted in part from the lack of knowledge of habitat and in part from a failure to recognize that some of the variability possibly is due to hybridization. The narrow-leaved specimens from Arkansas, Oklahoma, Texas and New Mexico, to which the epithets *S. sylvatica* var. *salicifolia* or *S. salicifolia* previously have been applied, is thought to be due to the influence of hybridization with *S. texana*, and as a result no nomenclatural status has been given them. The typical subspecies is largely confined to sandy areas within the coastal plain of the southern United States. It occurs only on limestone as a result of its putative hybridization with *S. texana*, and its occurrence on limestone soils is rather infrequent. *Stillingia sylvatica* ssp. *tenuis*, on the other hand, has become a stable entity on the limestone outcrops of extreme southeastern Florida.

Hybridization of *S. sylvatica* ssp. *sylvatica* with *S. aquatica* has been discussed under the heading of Subgeneric Categories. The following specimens of *S. sylvatica* in the herbarium of the Missouri Botanical Garden demonstrate the influence of introgressive hybridization with *S. aquatica*.

UNITED STATES: FLORIDA: OSCEOLA COUNTY: 5 mi. s.w. of Kissimee, dry sandy pineland, Rogers 4. HIGHLANDS COUNTY: n. of Highland, Hammock State Park, dry sands, Rogers 5; ½ mi. e. of Sebring, sandy flats, cleared field, Rogers 6; 2-3 mi. s.e. of Sebring, near shallow, marshy pond, Rogers 7. PALM BEACH COUNTY: 15 mi. s.w. of Lake Worth, sands near cypress swamp, Rogers 14-1, 14-3. MARTIN COUNTY: 1 mi. s. of Stuart, 100-200 yards from cypress pond, on a low sandy ridge, Rogers 15-1, 15-2, 15-3, 15-5, 15-7, 15-10, 15-11. (See also specimen citations of *S. aquatica* showing introgression with *S. sylvatica*, p. 230.)

The medicinal values of *S. sylvatica* have been explored and reported in several journals. An alcohol or water extract of the root was, and occasionally still is, used by physicians and laymen in South Carolina particularly, in the treatment of syphilis, in cutaneous diseases, chronic hepatic infections and in the composition of diet drinks.²³ As late as 1944²⁴, this plant was mentioned as of minor drug importance, particularly as a sialagogue and expectorant.

Vernacular names: Queen's Delight, Queen's Root, Silverleaf, Nettle Potato, Yaw-root, Marcory, and Cockup-hat.

18b. *STILLINGIA SYLVATICA* Garden, ex L. ssp. *tenuis* (Small) D. J. Rogers, stat. nov.

Stillingia tenuis Small in Bull. N. Y. Bot. Gard. 3:429. 1905. (T.: Small & Wilson 1580!).

Leaves very narrowly elliptic to linear, 2-10 cm. long, 0.3-1.0 cm. wide, apex acute. Bracts of the pistillate cymule caudate-acuminate.

²³Millsapugh, C. F. Medicinal Plants 1:151. 1892.

²⁴Allport, Noel L. The Chemistry and Pharmacy of Vegetable Drugs, p. 235, Tab. XVII. 1944.



Fig. 16. *Stillingia sylvatica* ssp. *tenuis*.

Confined to the extreme southeastern coast of Florida, usually growing only where limestone outcrops occur at the surface, with none or only a very slight amount of sandy soil mantle. Flowers from January to May or June, and fruits from March through June.

UNITED STATES: FLORIDA: Dade Co.

The subspecies occupies a distinct geographical and ecological region from its closest relative *S. sylvatica* ssp. *sylvatica*, but it has not sufficiently diverged to make it a separate species. This is perhaps due to the fact either that there is little possibility of further migration, it being limited to a very narrow strip on the southeast coast of Florida, or that insufficient time has elapsed since its formation. This part of Florida is one of the most recently exposed land masses on this continent.

Subgen. II. GYMNSTILLINGIA (Muell. Arg.) D. J. Rogers, stat. nov.

Gymnostillingia Muell. Arg. in *Linnaea* 32:89. 1863, as genus.

Series 4. ACUTIFOLIAE D. J. Rogers, ser. nov.

§ *Gymnostillingia* (Muell. Arg.) Pax & Hoffm. in *Engl. Pflanzenr.* IV. Fam. 147. V:193, 1912.

Frutices aut arbores parvi; sepalis floris pistillatis minutis vel inchoatis; flores staminales in cymula solitaria, polline sphaeroideo vel ellipsoideo; semina ecarunculata. Mexico australi et Guatemalae.

19. *STILLINGIA ACUTIFOLIA* (Benth.) Benth. ex Hemsl. *Biol. Centr.-Amer. Bot.* 3:135. 1883.

Sapum acutifolium Benth. *Pl. Hartweg.* 90. 1842. (T.: *Hartweg 614!*).

Gymnostillingia acutifolia (Benth.) Muell. Arg. in *Linnaea* 32:89. 1863.

Gymnostillingia macrantha Muell. Arg. loc. cit. 1863. (T.: *Pavon s. n.*),

Stillingia macrantha (Muell. Arg.) Benth. ex Hemsl. *Biol. Centr.-Amer. Bot.* 3:135. 1883,

Stillingia propria Brandg. in *Univ. Cal. Publ. Bot.* 6:185. 1915. (T.: *Purpus 7343!*).

Compact shrubs or small trees 1–7 m. tall; trunk to 12.5 cm. diameter below the lowest branches, the branches alternate to fascicled, terete below, angled above, the older branches sparsely lenticellate, the sap milky. Leaves alternate, petiolate, thinly membranaceous, dark green above, paler beneath, ovate, lanceolate, or elliptic, 2.8–15.0 cm. long, 1.0–4.3 cm. broad, acuminate, base acute, without cyathiform glands, the midrib and secondary venation prominent; petiole 2–5 mm. long. Inflorescence 2.5–4.2 cm. long, sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, not distinctly separate upon the peduncle; bracts of the pistillate and staminate cymules elliptic, cuspidate, about 1.5 mm. long, the glands patelliform, sessile. Sepals of the pistillate flower 3, minute or rudimentary; ovary sessile, 3-carpellate; styles about 2 mm. long. Staminate flowers solitary, very shortly pedicellate, about 2 mm. long, the calyx lobes entire; pollen ellipsoid to spheroid, triangular in cross-section with

3 pores, the exine finely punctate. Fruit 3-4 mm. wide, deeply 3-lobed, the lobes of the gynobase 1.5-2.0 mm. long; seeds about 3.5 mm. long, 2.5-3.0 mm. wide, with a slight depression on each side of the raphe at micropylar end, the base rounded, the testa smooth, the caruncle absent.

Mountainous regions of Chiapas and Guatemala in damp wooded regions, open banks, barrancas in pine forests, white sand slopes, at altitudes from 1400 to 3000 m. Flowers from late June to the first of September, and fruits from the first of August to the last of December.

MEXICO: CHIAPAS: Cerro del Boqueron, *Purpus* 7343 (F, GH, MO, NY); Siltepec, *Matuda* 1683 (A, MICH, NY).

GUATEMALA: CHIMALTENANGO: Volcan Acatenango, *Kellerman* 6576 (F); Chichavac, *Skutch* 29 (US), 554 (A); west of Patzun, *Williams & Molina* 11844 (F, MO); Alameda, *J. R. Johnston* 951 (F, NY); near Rio Pixcayo, between Chimaltenango and San Martin Jilotepeque, *Standley* 64330 (F); Barranco de La Sierra, southeast of Patzun, *Standley* 61510 (A, F, NY); near Parramos, *Standley* 59879 (A), 59880 (F); region of Los Positos, above Las Calderas, region of Las Calderas, *Standley* 57803 (A, F), 60018 (F), 80138 (A). GUATEMALA: Ruano 1256 (F); *Aguilar* 220 (F). HUEHUETENANGO: Todos Santos, *Melbus & Goodman* 3617 (F); San Juan Atitlan, *Skutch* 1165 (A, F, US). JALAPA: between Jalapa and Montana Miramundo, *Steyermark* 32895 (F). QUEZALTENANGO: Aguas Calientes, *Seler* 2741 (A, GH, NY, US); Cumbre de Tuilacan, s. w. of San Martin Chile Verde, *Standley* 67787 (F); region of Boxantin, s. e. of San Martin Chile Verde, *Standley* 83827 (F). SACATEPEQUEZ: along Rio Guacalate, on road between Antigua and Chimaltenango, *Standley* 81010 (F). SAN MARCOS: mountains along the road between San Marcos and Serchil, *Standley* 85327 (F); El Boqueron, near border of Dept. Quezaltenango, *Standley* 66284 (F); El Boqueron, in the mountains at the summit of the road between San Antonio Sacatepequez and Palestina, *Standley* 85280 (F); roadside, above Rio Tacana, near San Antonio, *Standley* 66165 (F). SANTA ROSA: Santa Rosa, *Heyde & Lux* 3473 (F, GH, NY, US). SOLOLA: Encuentros, *L. O. Williams* 13150 (F); Los Encuentros, *Seler* 2381 (GH, US). TOTONICAPAN: along road between San Francisco El Alto and Momostenango, *Standley* 84033 (F). AZCATEPEQUE: *Bernoulli & Cairo* 2499 (K, S). Dept. unknown, Hacienda de Argueta, *Hartweg* 614 (F, K).

According to information from a labeled specimen, the acrid milky sap of *S. acutifolia* is used as a caustic in the treatment of sores and boils.

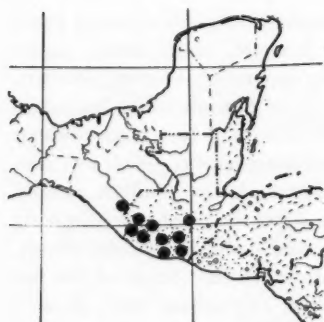


Fig. 17. *Stillingia acutifolia*.

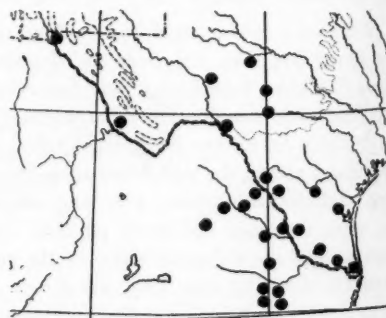


Fig. 18. *Stillingia Treculiana*.

Series 5. TRECULIANAE D. J. Rogers, ser. nov.

§ *Leptostachyae* Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:194. 1912.
 § *Gymnostillingia* Wats. in Pax & Hoffm., loc. cit. 1912, in synonymy.

Herbae perennes; flores pistillati sine sepalis (*S. Treculiana* excepta sepalis minutis et fagaceis); flores staminales in cymula solitaria, polline sphaeroideo segmentis 3 foraminibus 3; semina aut ecarunculata aut carunculis minutis et fugaceis.

KEY TO THE SPECIES

- A. Caruncle present; glands of pistillate bracts nearly sessile.
 B. Leaves obovate-spathulate, rounded or broadly acute, coarsely incised-dentate; sepals minute, fugacious; styles about 1 mm. long..... 20. *S. Treculiana*
 BB. Leaves linear, acuminate or acute, sparsely setulose-denticulate; sepals absent; styles about 4 mm. long..... 21. *S. paucidentata*
 AA. Caruncle absent; glands of pistillate bracts long-pedicellate.
 C. Leaves elliptic-spathulate, apex acuminate, finely callose-dentate, conspicuously 3-costate; stems striate..... 22. *S. spinulosa*
 CC. Leaves linear, apex acute, entire or sparsely denticulate, venation not prominent; stems terete..... 23. *S. linearifolia*
20. *STILLINGIA TRECULIANA* (Muell. Arg.) I. M. Johnston, in Contr. Gray Herb. n. s. 67:91. 1923.
- Sapium annuum* var. *dentatum* Torr. in Emory, Rept. U. S. & Mex. Bound. Surv. 2:201, 1859. (T.: Bigelow s. n.!).
Gymnanthes Treculiana Muell. Arg. in Linnaea 34:216. 1865. (T.: *Trecul* 1458!).
Sebastiania Treculiana (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1160. 1866.
Stillingia Torreyana S. Wats. in Proc. Am. Acad. 14:298. 1879. (Based on *Sapium annuum* var. *dentatum* Torr.).
Stillingia dentata (Torr.) Britt. & Rusby, in Trans. N. Y. Acad. 7:14. 1887.

Spreading perennial herbs 1.0–4.5 dm. tall; elongate tap root woody; fascicled branches arising from the ground level, striate, green. Leaves alternate, sessile, membranaceous, obovate-spathulate, 1.0–3.8 cm. long, 0.6–1.5 cm. wide, apex rounded to broadly acute, base narrowly cuneate, without cyathiform glands, coarsely incised-dentate, the midvein prominent, secondary venation obscure. Inflorescence 2.5–7.0 cm. long, pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, not distinctly separate upon the peduncle; bracts of the pistillate and staminate cymules elliptic or cuneate, concave, with 1–3 mucros, the patelliform glands nearly sessile. Pistillate flowers solitary, sepals minute, fugacious; ovary sessile, 3-carpellate; styles about 1 mm. long. Staminate flowers solitary, subsessile, about 1.5 mm. long; calyx deeply 2-lobed, the margins involute, entire; pollen spheroid, deeply 3-segmented, with 3 pores, the exine coarsely punctate. Fruit deeply 3-lobed, the lobes of the gynobase 0.8–1.0 mm. long; seeds about 2.5 mm. long, 1.5–2.0 mm. wide, with a slight depression on each side of the raphe at the micropylar end, the base rounded, the testa smooth or slightly rugulose, the caruncle present.

Sandy soils with limestone base, gravel, on hills, mesas, grasslands, along railroads and roadsides in southwestern Texas and northeastern Mexico. Flowers from the last of February to the first of June, and fruits from the last of March through the first of August.

UNITED STATES: TEXAS: Bexar, Cameron, Concho, Crockett, Presidio, Star, Tom Green, Val Verde, and Webb counties.

MEXICO: COAHUILA: Allende, *Marsh* 1768 (F); Muzquiz, *Marsh* 1116 (F); Cuatro Ciénegas, *Sbrevé* 8454 (UC); Sabinas, M. E. Jones 29115 (MO, UC). NUEVO LEON: Mesas, García, *Pringle* 2504 (F, GH, MO, NY, UC, US); 100 kilo. s. of Nuevo Laredo, on road to Monterrey, *Frye & Frye* 2375 (GH, MO, NY, US); near Santa Catarina, Alonís, Johnson & Barkley 15189M (F, GH, MO, TEX); 23 mi. n. of Sabinas Hidalgo, Barkley & Webster 14497 (MO, TEX, UC); canyon 12 mi. w. of Monterrey, Barkley & Painter 14253 (GH, MO, TEX); 10 mi. w. of Monterrey, *Sbrevé & Tinkham* 9572 (GH); Rancho Resendez, Lampazos, Edwards 389 (F, MO, TEX, UC); Monterrey, E. Palmer 1258 (GH, US). TAMAULIPAS: San Miguel, *Pringle* 2071 (F). Mexico orientali ad Rio Bravo del Norte, *Trecul* 1458 (MO, P).

There has been some confusion as to whether *S. Treculiana* is an annual or perennial. This confusion arose from the original description of *Sapium annuum* var. *dentatum* made by Torrey. He could easily have called this plant an annual since the specimen used as a type was a small fragment, without roots. Mueller, however, definitely states in his description of *Gymnanthes Treculiana* that this is a perennial species. Examination of material from several herbaria amply corroborates his observation.

Vernacular name: Yerba del Sapo (Mexico).

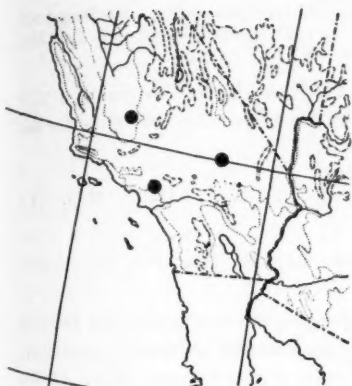
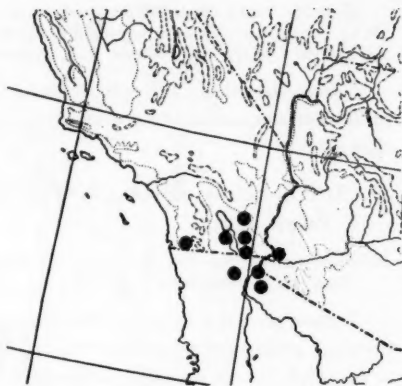
21. *STILLINGIA PAUCIDENTATA* S. Wats. in Proc. Am. Acad. 14:298. 1879. (T.: E. Palmer 517!).

Stillingia linearifolia var. *paucidentata* (S. Wats.) Jepson, Fl. Cal. 2¹:422. 1936.

Compact, erect perennial herbs 2.5–3.5 dm. tall; elongate tap root woody; the fasciated branches arising from ground level, secondary branches alternate to approximate. Leaves alternate to approximate, sessile, crowded, membranaceous, linear, 2–4 cm. long, 0.1–0.3 cm. wide, acuminate or acute, not narrowed at the base, without cyathiform glands, sparsely setulose-denticulate to entire, the mid-vein prominent, decurrent, secondary venation obscure. Inflorescence 2.3–7.0 cm. long, usually sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, not distinctly separate upon the peduncle; bracts of the pistillate and staminate cymules elliptic or cuneate, mucronulate, the patelliform glands short-pedicellate (less than 1 mm.). Pistillate flowers solitary; sepals absent; ovary sessile, 3-carpellate; styles about 4 mm. long. Staminate flowers solitary, subsessile, about 1.5 mm. long; calyx shallowly 2-lobed, the lobes slightly serrulate; pollen spheroid, shallowly 3-segmented, with 3 pores, the exine coarsely punctate. Fruit deeply 3-lobed, the lobes of the gynobase 1.5–2.0 mm. long; seeds about 3 mm. long, 2 mm. wide, testa smooth, the caruncle small.

In sandy washes, plains, bare arid hills and gravel, up to 4000 ft. altitude. Flowers from the first of April through the end of May, and fruits about the first of May through the middle of June.

UNITED STATES: CALIFORNIA: Kern, Los Angeles, and San Bernardino counties.

Fig. 19. *Stillingia paucidentata*.Fig. 20. *Stillingia spinulosa*.

22. *STILLINGIA SPINULOSA* Torr. in Emory, Notes Milit. Rec. 151. 1848. (T.: Emory s. n.).

Sapium annuum Torr. in Emory, Rept. U. S. & Mex. Bound. Surv. 2:201. 1859. (Based on *S. spinulosa*).

Stillingia annua (Torr.) Muell. Arg. in DC. Prodr. 15²:1160. 1866.

Compact perennial herbs 0.5–2.0 dm. tall; elongate tap root woody, the fascicled branches arising from ground level, the secondary branches opposite or approximate. Leaves opposite or approximate, sessile, crowded, membranaceous, elliptic-spathulate, 1.5–4.0 cm. long, 0.5–1.7 cm. wide, apex acuminate, base narrowly cuneate, without cyathiform glands, finely callose-dentate, decurrent, prominently 3-costate. Inflorescence 1.2–2.0 cm. long, usually sessile below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, crowded, not distinctly separate upon the peduncle; bracts of pistillate and staminate cymules broadly elliptic, concave, cuspidate, somewhat 3-lobed, about 1 mm. long, the patelliform glands pedicellate, 1.5–2.0 mm. long. Pistillate flowers solitary, sepals absent; ovary sessile, 3-carpellate; styles about 3 mm. long. Staminate flowers solitary, subsessile, about 1.5 mm. long; calyx shallowly 2-lobed, the lobes entire; pollen ellipsoid, triangular in cross-section, with 3 pores, the exine finely to coarsely punctate. Fruit deeply 3-lobed, the lobes of the gynobase about 2 mm. long; seeds 3.0–3.5 mm. long, the testa smooth, sometimes mottled, the caruncle absent.

Sandy open desert. Flowers from late December to late March, and fruits from March to June.

UNITED STATES: ARIZONA: Yuma Co. CALIFORNIA: San Diego, Riverside, Imperial, and San Bernardino counties.

MEXICO: BAJA CALIFORNIA: mesa near Cerro Breto, Cucapa Mts., *MacDougal* 206 (NY). SONORA: Colonia Lerdo, *MacDougal* s. n. (NY); Buena Mesa near Col. Riv., *MacDougal* s. n. (NY); Pimeria Alta, *Schott* s. n. (NY).

Torrey described *Stillingia spinulosa* in 1848, but changed the name in 1859 to *Sapium annuum*, using the same specimens. No explanation was given for this change.

23. *STILLINGIA LINEARIFOLIA* S. Wats. in Proc. Am. Acad. 14:297. 1879. (T.: *E. Palmer* 449!).

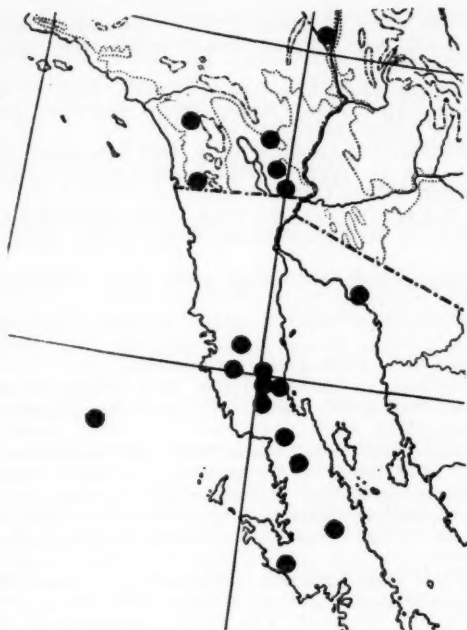
Stillingia gymnogyna Pax & Hoffm. in Engl. Pflanzenr. IV. Fam. 147. V:196. 1912. (Based on *S. linearifolia* S. Wats.).

Diffuse perennial herbs 1.5–9.0 dm. tall; elongate tap root woody, the fascicled branches arising from ground level, the secondary branches alternate, approximate, or fascicled. Leaves alternate or approximate, sessile, membranaceous, linear, 1.2–3.2 cm. long, 0.1–0.3 cm. wide, apex acute, the base narrowly acute, without cyathiform glands, entire or sparsely denticulate, shortly decurrent, the venation not prominent. Inflorescence 1.6–7.0 cm. long, sessile or shortly pedunculate below the lowest pistillate cymule, the upper staminate and lower pistillate cymules spiral, scattered, not distinctly separate upon the peduncle; bracts of the pistillate and staminate cymules rhombic or cuneate, mucronulate, flattened, about 1 mm. long, the cyathiform glands pedicellate, about 1 mm. long. Pistillate flowers solitary; sepals absent; ovary sessile, 3-carpellate; styles about 2 mm. long. Staminate flowers solitary, subsessile, about 1 mm. long; calyx shallowly 2-lobed, the lobes entire or slightly serrulate; pollen spheroid to irregularly ellipsoid, broadly triangular in cross-section, with 3 pores, the exine finely punctate. Fruit deeply 3-lobed, the lobes of the gynobase about 1 mm. long; seeds about 1.8–2.5 mm. long, 1.5–1.8 mm. wide; testa smooth, sometimes mottled, the caruncle absent.

Desert sands, lava rocks, chaparral, dry sandy washes, and sandy roadsides. Flowers from the first of March to the end of April, and fruits from the middle of March to the middle of June.

UNITED STATES: CALIFORNIA: Imperial, Los Angeles, Riverside, San Bernardino, and San Diego counties. NEVADA: Clark Co.

MEXICO: BAJA CALIFORNIA: sandy arroyo margin, San Augustin, *Gentry* 4004 (GH, MO, UC); 11 km. s.e. of San Augustin on road to Catavina, *Carter, Alexander & Kellogg* 1877 (MO); lagoon head, Guadalupe Island, *E. Palmer* 785 (F, GH, US); 37 mi. s. of Pozo Aleman, *Shreve* 7018 (F, MICH, US); sandy plains, Calmalli, *Purpus* 25 (F, US); Yecate, *Orcutt* s. n. (F, MO), Socorri, *Orcutt* s. n. (F, MO); coast near Ascension Island, *Brandegee* s. n. (UC); Cordon Grande, *Brandegee* s. n. (F, GH); lava rocks, San Quintin, *Epling & Stewart* s. n. (F, US); south slope 8 mi. from Rosario on road to El Marmol, *Wiggins* 4337 (GH, US); sandy wash at junction of El Marmol and San Fernando roads, 25 mi. from El Marmol, *Wiggins* 4354 (GH, MICH, NY, UC, US); sandy flats 32 mi. s. of Pozo Aleman, *Wiggins* 7880 (F, MICH, NY, UC, US); sandy wash 11 mi. e. of San Ignacio, *Wiggins* 7913 (F, MICH, NY, UC, US); along Rio Santo Domingo about 4 miles above the Mission, *Wiggins & Demaree* 4778 (F, GH, MICH, NY, UC, US). SONORA: 30 mi. s. w. of Sonoyta on road to Punta Penasco, *Shreve* 7591 (F, MICH, MO, US); llano 30 mi. from Sonoyta, *Wiggins* 8359 (MICH, UC, US); 28 mi. s. of Sonoyta on road to Punta Penasco, *Keck* 4183 (NY).

Fig. 21. *Stillingia linearifolia*.

DOUBTFUL SPECIES

Stillingia cruenta Standl. & Steyerl. in Field Mus. Publ. Bot. 23:125. 1944. (T.: Standley 91207!).

Without exception, the available specimens of this species are sterile. It will be impossible to assign the plant to a genus until flowering or fruiting specimens are available.

EXCLUDED SPECIES

In the following list, the species marked with an exclamation point (!) have been verified by examination either of the type specimen or of a photograph of the type, but those without an exclamation point are excluded only on the authority of Pax and Hoffmann in Engl. Pflanzenr. IV, Fam. 147, V:197. 1912. Only those species found in the Americas are considered here. Old World species have not been included. No reference is made to Baillon's 'Étud. Gén. Euphorb.' 1858, since Baillon rarely made formal transfers, although his taxonomy included many genera under *Stillingia*.

S. appendiculata Muell. Arg. in Linnaea 32:87. 1863 = *SAPIUM APPENDICULATUM* (Muell. Arg.) Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:214. 1912!

S. arborea Pav. ex Huber in synonym. = *SAPIUM PEDICELLATUM* Huber, in Bull. Herb. Boiss. II, 6:352, f. 9. 1906.

- S. arborescens* Pittier, Contr. Fl. Venez. 9. 1921 = *SEBASTIANIA GRANATENSIS* (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1189. 1866! (*Gymnanthes granatensis* Muell. Arg. in Linnaea 32:107. 1863).
- S. babiensis* (Muell. Arg.) Baill. in Adansonia 5:329. 1865 (*Gymnanthes babiensis* Muell. Arg. in Linnaea 32:102. 1863) = *SEBASTIANIA BAHIENSIS* (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1183. 1866!
- S. bidentata* (Mart.) Baill. in Adansonia 5:324. 1865 (*Cnemidostachys bidentata* Mart. Nov. Gen. & Sp. 1:69, t. 43. 1824) = *SEBASTIANIA BIDENTATA* (Mart.) Pax in Engl. Pflanzenr. IV, Fam. 147, V:113. 1912.
- S. biglandulosa* (L.) Baill. in Adansonia 5:320. 1865 (*Hippomane biglandulosa* L. Sp. Pl. ed. 2, 1431. 1763) = *SAPIUM HIPPOMANE* G. F. W. Mey. Prim. Fl. Essequib. 275, 1818.
- S. brasiliensis* (Spreng.) Baill. in Adansonia 5:328. 1865 = *SEBASTIANIA BRASILIENSIS* Spreng. Neue Entdeck. 2:118, t. 3. 1821.
- S. brevifolia* (Kl. ex Muell. Arg.) Baill. in Adansonia 5:328. 1865 (*Gymnanthes brevifolia* Kl. ex Muell. Arg. in Linnaea 32:104. 1863) = *SEBASTIANIA BREVIFOLIA* (Kl. ex Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1186. 1866.
- S. Commersoniana* Baill. in Adansonia 5:330. 1865 = *SEBASTIANIA KLOTZSCHIANA* (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1178. 1866 (*Gymnanthes Klotzschiana* Muell. Arg. in Linnaea 32:98. 1863).
- S. concolor* (Spreng.) Baill. in Adansonia 5:327. 1865 (*Gussonia concolor* Spreng. Neue Entdeck. 2:120, t. 2. 1821) = *ACTINOSTEMON CONCOLOR* (Spreng.) Muell. Arg. var. κ . *GENUINUS* Muell. Arg. in Mart. Fl. Bras. 11²:595, t. 595, f. II. 1874.
- S. coriacea* (Mart.) Baill. in Adansonia 5:323. 1865 (*Cnemidostachys coriacea* Mart. Nov. Gen. & Sp. 1:71. 1824) = *SEBASTIANIA MARGINATA* (Mart.) Muell. Arg. in DC. Prodr. 15²:1166. 1866.
- S. corniculata* (Vahl) Baill. Étud. Gén. Euph. Atlas, pl. 8, fig. 1-12. 1858 (*Tragia corniculata* Vahl, Eclog. Amer. 2:55, t. 19. 1789) = *SEBASTIANIA CORNICULATA* (Vahl) Pax in Engl. Pflanzenr. IV, Fam. 147, V:96. 1912, *SEBASTIANIA GLANDULOSA* (Mart.) Pax, loc. cit. 100. 1912, *SEBASTIANIA HISPIDA* (Mart.) Pax, loc. cit. 105. 1912.
- S. cremostachya* Baill. in Adansonia 5:322. 1865 = *SAPIUM KLOTZSCHIANUM* (Muell. Arg.) Huber, in Bull. Herb. Boiss. II, 6:438, f. 30. 1906 (*Sapium biglandulosum* var. ϵ . *Klotzschianum* Muell. Arg. in Linnaea 32:117. 1863).
- S. daphniphylla* Baill. in Adansonia 5:326. 1865 = *SEBASTIANIA DAPHNIPHYLLA* (Baill.) Muell. Arg. in DC. Prodr. 15²:1180. 1866.
- S. discolor* (Spreng.) Baill. in Adansonia 5:327. 1865 (*Gussonia discolor* Spreng. Neue Entdeck. 2:119, t. 2, f. 7-10. 1821) = *SEBASTIANIA DISCOLOR* (Spreng.) Muell. in DC. Prodr. 15²:1185. 1866!
- S. divaricata* Kl. ex Pax & Hoffm. in synon. in Engl. Pflanzenr. IV, Fam. 147, V:230. 1912 = *SAPIUM MORITZIANUM* Kl. in Seem. Bot. Voy. Herald, 100. 1852.
- S. dracunculoides* Baill. in Adansonia 5:321. 1865 = *EXCOECARIA BIGLANDULOSA* var. ρ . *DRACUNCULOIDES* (Baill.) Muell. Arg. in DC. Prodr. 15²:1207. 1866.
- S. eglandulosa* Rich. in Sagra, Hist. Fis. Cuba 11:202. 1850 = *GRIMMEODENDRON EGLANDULOSUM* (Rich.) Urb. Symb. Antill. 5:398. 1908!
- S. frutescens* Bosc. ex Steud. Nomencl. Bot. 1:815. 1821 = *SEBASTIANIA FRUTICOSA* (Bartr.) Fern. in Rhodora 46:45. 1944.
- S. fruticosa* Michx. ex Spreng. Syst. 3:805. 1826 = *SEBASTIANIA FRUTICOSA* (Bartr.) Fern. in Rhodora 46:45. 1944.
- S. Gaudichaudii* (Muell. Arg.) Baill. in Adansonia 5:332. 1865 = *SEBASTIANIA GAUDICHAUDII* (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1177. 1866!
- S. glabrata* (Mart.) Baill. Étud. Gén. Euphorb. Atl. 17, pl. 8, figs 13-16. 1858 (*Cnemidostachys glabrata* Mart. Nov. Gen. & Sp. 1:70. 1824) = *SEBASTIANIA MULTIRAMEA* (Kl.) Muell. Arg. var. β . *GLABRATA* (Mart.) Pax in Engl. Pflanzenr. IV, Fam. 147, V:120. 1912!
- S. glandulosa* Dombey ex Juss. in Ann. Sci. Nat. Bot. 25:24. 1832 = *ADENOPELTIS COLLIGUAYA* Bert. ex Juss. loc. cit. 1832.

- S. guianensis* (Aubl.) Baill. in Adansonia 5:332. 1865 = *MAPROUNEA GUIANENSIS* Aubl. Hist. Pl. Guian. 2:895, t. 342. 1775.
- S. buematantiba* Standl. in Ann. Mo. Bot. Gard. 27:314. 1940 = *SAPIUM MORITZIANUM* Kl. in Seem. Bot. Voy. Herald, 100. 1852!
- S. bastata* Kl. ex Baill. in Adansonia 5:324. 1865 = *SEBASTIANIA DITASSOIDES* (Didrichs.) Muell. Arg. var. β . *GLABRATA* Muell. Arg. in DC, Prodr. 15²:1174, 1866!
- S. heterodoxa* Muell. Arg. in Linnæa 32:89. 1863 = *SEBASTIANIA HETERODOXA* (Muell. Arg.) Benth. in Benth. & Hook. f. Gen. Pl. 3:334. 1880!
- S. hilariana* Baill. in Adansonia 5:332. 1865 = *MAPROUNEA BRASILIENSIS* St. Hil. Pl. Usuel. Bresil, t. 65. 1824-1828.
- S. hypoleuca* (Benth.) Baill. in Adansonia 5:330. 1865 = *GYMNANTHES HYPOLEUCA* Benth. in Hook. Jour. Bot. 6:325. 1854!
- S. jacobinensis* (Muell. Arg.) Baill. in Adansonia 5:329. 1865 = *SEBASTIANIA JACOBINENSIS* (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1188. 1866.
- S. laureola* Baill. in Adansonia 5:327. 1865 = *SEBASTIANIA LAUREOLA* (Baill.) Muell. Arg. in DC. Prodr. 15²:1180. 1866.
- S. laurifolia* Rich. in Sagra, Hist. Fis. Cuba 11:201, pl. 69. 1850 = *SAPIUM JAMAICENSE* Swartz, Adnot. Bot. 62. 1829.
- S. ligustrina* Michx. Fl. Bor. Amer. 2:213. 1803 = *SEBASTIANIA FRUTICOSA* (Bartr.) Fern. in Rhodora 46:45. 1944.
- S. marginata* (Muell. Arg.) Baill. in Adansonia 5:321. 1865 = *SAPIUM MARGINATUM* var. α . *LANCEOLATUM* Muell. Arg. in Linnæa 32:120. 1863!
- S. multiramea* (Kl.) Baill. in Adansonia 5:325. 1865 (*Serothrostachys multiramea* Kl. in Wieg. (Erichs.) Arch. 7:185. 1841) = *SEBASTIANIA MULTIRAMEA* (Kl.) Muell. Arg. var. β . *GLABRATA* (Baill.) Pax in Engl. Pflanzenr. IV, Fam. 147, V:120. 1912!
- S. myrtilloides* (Mart.) Baill. in Adansonia 5:323. 1865 (*Cnemidostachys myrtilloides* Mart. Nov. Gen. & Sp. 1:67, t. 40. 1824) = *SEBASTIANIA MYRTILLOIDES* (Mart.) Pax in Engl. Pflanzenr. IV, Fam. 147, V:93. 1912, *SEBASTIANIA OLEOIDES* (Mart.) Muell. Arg. in Mart. Fl. Bras. 11²:548. 1874!
- S. nervosa* (Muell. Arg.) Baill. in Adansonia 5:328. 1865 (*Gymnanthes nervosa* Muell. Arg. in Linnæa 32:102. 1863) = *SEBASTIANIA NERVOSA* (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1183. 1866!
- S. obovata* (Kl. ex Muell. Arg.) Baill. in Adansonia 5:321. 1865 = *SAPIUM OBOVATUM* Kl. ex Muell. Arg. in Linnæa 32:120. 1863.
- S. pachystachya* (Kl.) Baill. in Adansonia 5:330. 1865 (*Adenogyne pachystachys* Kl. in Wieg. (Erichs.) Arch. 7:184. 1841) = *SEBASTIANIA PACHYSTACHYS* (Kl.) Muell. Arg. in DC. Prodr. 15²:1182. 1866!
- S. patagonica* (Spegazz.) Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:188. 1912 (*Colliguaya patagonica* Spegazz. in Revist. Facult. Agron. y Veter. La Plata 3:572. 1907) = *SAPIUM PATAGONICUM* (Spegazz.) D. J. Rogers, comb. nov.
- This species has very few affinities with any other known species of *Sapium*, *Stillingia* or *Colliguaya*. However, the absence of a gynobase, the axillary inflorescence, the structure of the staminate flower, the shape of the glands at the base of the leaf blade all point to characters of *Sapium*, not *Stillingia*. In one character, the texture of the seed coat, this species shows no affinities with the American species of *Sapium*. All of the new world species of *Sapium* have an arillate seed coat, but *S. patagonicum* has a firm, hardened testa, without evidence of an aril.
- S. phyllanthiformis* Baill. in Adansonia 5:331. 1865 = *SEBASTIANIA SCHOTTIANA* Muell. Arg. var. β . *PHYLLANTHIFORMIS* (Baill.) Pax & Hoffm. in Engl. Pflanzenr. IV, Fam. 147, V:127. 1912.
- S. prostrata* (Mart.) Baill. in Adansonia 5:324. 1865 (*Cnemidostachys prostrata* Mart. Nov. Gen. & Sp. 1:70. 1824) = *SEBASTIANIA CORNICULATA* (Vahl) Pax, var. ν . *PROSTRATA* (Mart.) Muell. Arg. in DC. Prodr. 15²:1172. 1866!, *SEBASTIANIA GLANDULOSA* (Mart.) Pax, in Engl. Pflanzenr. IV, Fam. 147, V:100. 1912, and *SEBASTIANIA HISPIDA* (Mart.) Pax, loc. cit. 105. 1912.

- S. pteroclada* (Muell. Arg.) Baill. in Adansonia 5:329. 1865 (*Gymnanthes pteroclada* Muell. Arg. in Linnaea 32:107. 1863) = SEBASTIANIA PTEROCLADA (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1190. 1866!
- S. ramosissima* (St. Hil.) Baill. in Adansonia 5:328. 1865 (*Microstachys ramosissima* St. Hil. Hist. Pl. Remarq. Bresil. 242. 1824) = SEBASTIANIA BRASILIENSIS Spreng. Neue Entdeck. 2:118, t. 3. 1821.
- S. rigida* (Muell. Arg.) Baill. in Adansonia 5:330. 1865 (*Gymnanthes rigida* Muell. Arg. in Linnaea 32:99. 1863) = SEBASTIANIA RIGIDA (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1180. 1866.
- S. rufescens* Moritz ex Pax & Hoffm. in synonym. in Engl. Pflanzenr. IV, Fam. 147, V:212. 1912 = SAPIUM STYLARE Muell. Arg. in Linnaea 32:119. 1863.
- S. salicifolia* Kl. ex Baill. in Adansonia 5:320. 1865 = SAPIUM HAEMATOSPERMUM Muell. Arg. in Linnaea 34:217. 1865.
- S. Schottiana* (Muell. Arg.) Baill. in Adansonia 5:331. 1865 (*Gymnanthes Schottiana* Muell. Arg. in Linnaea 32:96. 1863) = SEBASTIANIA SCHOTTIANA (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1176. 1866!
- S. sebifera* (L.) Michx. Fl. Bor. Amer. 2:213. 1803 (*Croton sebiferum* L. Sp. Pl. ed. 1, 1004. 1753) = SAPIUM SEBIFERUM (L.) Roxb. Fl. Ind. 3:693. 1832.
- S. serrata* Kl. ex Baill. in Adansonia 5:329. 1865 = SEBASTIANIA SERRATA (Kl. ex Baill.) Muell. Arg. in Mart. Fl. Bras. 11²:576. 1874.
- S. serrulata* (Mart.) Baill. in Adansonia 5:324. 1865 (*Cnemidostachys serrulata* Mart. Nov. Gen. & Sp. 1:68, t. 42. 1824) = SEBASTIANIA SERRULATA (Mart.) Muell. Arg. var. a. KLOTZSCHIANA Muell. Arg. in DC. Prodr. 15²:1167. 1866!
- S. stipulacea* (Kl. ex Muell. Arg.) Baill. in Adansonia 5:325. 1865 (*Gymnanthes stipulacea* Kl. ex Muell. Arg. in Linnaea 32:96. 1863) = SEBASTIANIA STIPULACEA (Kl. ex Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1176. 1866!
- S. sylvatica* Garden var. *paraguayensis* Morong, in Ann. N. Y. Acad. 7:226. 1893 = SAPIUM HAEMATOSPERMUM Muell. Arg. in Linnaea 34:217. 1865!
- S. trinervia* (Muell. Arg.) Baill. in Adansonia 5:328. 1865 (*Gymnanthes trinervia* Muell. Arg. in Linnaea 32:101. 1863) = SEBASTIANIA TRINERVIA (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1182. 1866!
- S. Weddelliana* Baill. in Adansonia 5:329. 1865 = SEBASTIANIA WEDDELLIANA (Baill.) Muell. Arg. in DC. Prodr. 15²:1188. 1866.
- S. Widgreni* (Muell. Arg.) Baill. in Adansonia 5:326. 1865 (*Gymnanthes Widgreni* Muell. Arg. in Linnaea 32:97. 1863) = SEBASTIANIA WIDGRENI (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1178. 1866.
- S. ypanemensis* (Muell. Arg.) Baill. in Adansonia 5:330. 1865 (*Gymnanthes ypanemensis* Muell. Arg. in Linnaea 32:100. 1863) = SEBASTIANIA YPANEMENSIS (Muell. Arg.) Muell. Arg. in DC. Prodr. 15²:1179. 1866!

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Italicized numerals refer to collector's numbers, *s. n.* (*sine numero*) to unnumbered collections; parenthetical numerals refer to the numbers of taxonomic entities conserved in this revision.

- | | |
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| Aguilar, I. 93, 1314 (16); 220 (19); 760, 1106 (6). | Arnold, L. E., & West, E. 16017, 16018, 41527 (18a). |
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| Alonis, T., Johnson, J. C., & Barkley, F. A. 15189M (20). | Ashe, W. W. <i>s. n.</i> (18a); <i>s. n.</i> (8). |
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	<i>Klotzschiana</i>	250	<i>daphniphylla</i>	250
23).	<i>nervosa</i>	251	<i>discolor</i>	250
	<i>pteroclada</i>	252	<i>ditassoides</i> var. <i>glabrata</i>	251
	<i>rigida</i>	252	<i>fruticosa</i>	250, 251
	<i>Schottiana</i>	252	<i>Gaudichaudii</i>	250
	<i>stipulacea</i>	252	<i>glandulosa</i>	250, 251
9).	<i>Treculiana</i>	246	<i>granatensis</i>	250
(6);	<i>trinervia</i>	252	<i>heterodoxa</i>	251
s. n.	<i>Widgreni</i>	252	<i>hispida</i>	250, 251
	<i>ypanemensis</i>	252	<i>jacobinensis</i>	251
524	<i>Gymnostillingia</i>	208, 243	<i>Klotzschiana</i>	250
	<i>acutifolia</i>	243	<i>laureola</i>	251
	<i>loranthacea</i>	232	<i>marginata</i>	250
	<i>macrantha</i>	243	<i>multiramea</i> var. <i>glabrata</i>	250, 251
607	<i>Hippomane biglandulosa</i>	250	<i>myrtilloides</i>	251
	<i>Maprounea</i>	209	<i>nervosa</i>	251
	<i>brasiliensis</i>	251	<i>oleoides</i>	251
(8a).	<i>guianensis</i>	251	<i>pachystachys</i>	251
0).	<i>Microstachys ramosissima</i>	252	<i>pteroclada</i>	252
	<i>Sapium</i>	207, 209	<i>rigida</i>	252
	<i>acutifolium</i>	243	<i>Schottiana</i>	252
(17).	<i>annuum</i>	247	var. <i>phyllanthiformia</i>	251
	var. <i>dentatum</i>	246	<i>serrata</i>	252
	<i>appendiculatum</i>	249	<i>serrulata</i> var. <i>Klotzschiana</i>	252
	<i>biglandulosum</i> var. <i>Klotzschianum</i>	250	<i>stipulacea</i>	252
	<i>Bodenbenderi</i>	222	<i>Treculiana</i>	245
	<i>cupuliferum</i>	234	<i>trinervia</i>	252

Weddelliana	252	laureola	251
Widgreni	252	laurifolia	251
ypanemensis	252	Leptostachyae (section)	245
Seborium	219	ligustrina	251
Stillingia	207, 219	linearifolia	213, 248, 249
acutifolia	208, 212, 218, 243, 244	linearifolia	238
ACUTIFOLIAE (series)	210, 215, 217, 218, 243	var. paucidentata	246
angustifolia	238, 240	lorantbacea	232
annua	247	macrantha	243
appendiculata	249	marginata	251
aquatica	211, 213, 215, 216, 229, 241	microperma	225, 226
arborea	249	multiramea	251
arborescens	250	myrtilloides	251
babiensis	250	nervosa	251
bicaupellaris	212, 228	obovata	251
bidentata	250	oppositifolia	210, 212, 220
biglandulosa	250	OPPOSITIFOLIAE (series)	210, 213, 215, 216, 218, 220
Bodenbenderi	211, 215, 222	Pachycladae (section)	230
brasiliensis	250	pachystachya	251
brevifolia	250	patagonica	251
Commersoniana	250	paucidentata	213, 214, 246, 247
concolor	250	peruviana	211, 223
coriacea	250	phyllanthiformis	251
corniculata	250	propria	243
cremostachya	250	prostrata	251
cruenta	249	pteroclada	252
daphniphylla	250	ramosissima	252
dentata	245	rigida	252
dichotoma	232	rufescens	252
DICHOTOMAE (series)	210, 212, 213, 216, 217, 230	salicifolia	235, 240
diphtherina	211, 226, 227, 228	salicifolia	239, 240, 252
discolor	250	salpingadenia	211, 215, 234
divaricata	250	salpingadenia	
dracunculoides	250	ssp. anadena	234
Dusenii	212, 215, 236	var. cupulifera	234
eglandulosa	250	var. salicina	234
Eustillingia (section)	220	ssp. saxatilis	235
frutescens	250	var. angustior	235
fruticosa	250	var. elliptica	235
Fruticosae (section)	220	var. grandifolia	235
Gaudichaudii	250	sanguinolenta	211, 224, 225
glabrata	250	var. angustifolia	224
glandulosa	250	var. lanceolata	224
guianensis	251	saxatilis	212, 232
gymnogyna	248	saxatilis	235
GYMNOSTILLINGIA (subgenus)	210, 212, 213, 214, 215, 243	var. grandifolia	235
Gymnostillingia (section)	243, 245	var. salicifolia	215, 235
baematantha	251	f. angustior	235
bastata	251	f. latior	235
heterodoxa	251	Schottiana	252
Hilariana	251	scutellifera	211, 215, 235
hypoleuca	251	sebifera	252
jacobinensis	251	serrata	252
lanceolata	239	serrulata	252
		Smallii	240
		spathulata	240

spinulosa	213, 247
STILLINGIA (subgenus)	210, 212, 213, 214, 220
stipulacea	252
sylvatica	213, 215, 219, 239, 240
ssp. sylvatica	211, 239
ssp. tenuis	215, 241, 242
sylvatica	
var. angustifolia	239
var. genuina	239
var. linearifolia	238
var. paraguayensis	252
var. salicifolia	239
var. spatbulata	239
Sylvaticae (section)	233
SYLVATICAE (series)	210, 214, 215, 217, 233

tenuis	241
texana	238
var. latifolia	238
var. typica	238
Torreyana	245
trapezoidea	217, 231
Treculiana	244, 245
TRECVLIANA (series)	210, 215, 217, 218, 245
trinervia	252
Uleana	213, 231
Weddelliana	252
Widgreni	252
ypanemensis	252
zelayensis	214, 217, 218, 236, 238
Stillingiinae	209
Tragia corniculata	250

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THE RECENT INTRUSION OF FORESTS IN THE OZARKS

AUGUST P. BEILMANN* AND LOUIS G. BRENNER**

INTRODUCTION

Scanlan (1950), in writing of American forests, says: "The lumber barons began to despoil and they did an excellent job." This statement might correctly be applied to a specific region but a lumber baron could not operate in a prairie region. Seemingly, it cannot be applied at all to the eastern and northern portions of the Ozarks. Within historic times this vast region was a prairie, or at least park-like in that the trees were widely spaced and confined to the water-courses and drainage-ways. The logging operations which are now so much a part of the industry of the Ozark region are but little more than a century old. The loggers have been, and still are, cutting the first crop of trees to mature there. In some sections any tree large enough to yield a 2 x 4 is cut; and the region will be scoured again and again for more trees of that size. However, there is evidence to show that insufficient time has elapsed to develop a mature second growth of either pine or hardwoods.

During a study of the flora of the northeastern edge of the Ozark Uplift an effort was made to visualize the steps which are supposed to precede the formation of a mature forest—the "climax" of the ecologist. This time-elapse study of only twelve years revealed a speeding succession of plant species not at all approaching the accepted trial-and-error elimination which is supposed to set the pattern for our forest areas. In an effort to reconstruct the Ozark forest before the advent of the white settlements and before logging had progressed very far, a search was made for old trees. After considerable difficulty many old trees were found which bridged the gap between grassland and forests. In one detailed study of a relic (Beilmann, 1943), a ring count gave an estimated age of 327 years. This was a "wolf" tree with heavy lateral branches whose tips touched the ground; it had grown as an isolated specimen and only recently had it any neighbors.

ECOLOGY

Steyermark (1940) made the first critical study of plant successions in the Ozarks. He found and described 164 examples of "large-scale natural plots." According to him, the classical Maple-Beech Climax, as proposed by Clements and Weaver (1929) on the basis of climatic conditions, does not hold in this area. For this he would substitute five edaphic associations based on the physical, chemical, and local moisture conditions. It would seem to be quite difficult to find such vast variation in soils that one might find 164 "associations" based on edaphic conditions alone, unless a certain immaturity was a characteristic of the forest aspect. Steyermark devotes one chapter to "variations induced by burning, logging,

*Manager, Missouri Botanical Garden Arboretum.

**Assistant Manager, Missouri Botanical Garden Arboretum.

clearing, and other unnatural causes." For centuries, burning, aggravated by reduced precipitation, governed the distribution of forests. As the area became settled, the decrease in wild fires and the increase in rainfall reduced the loss by fire. Logging and clearing followed, but logging reached its peak in 1900. Therefore, the unnatural causes listed by Steyermark, together with edaphic adaptations, govern the distribution of species in the Ozarks. The writings of the earlier travelers indicate that not nearly enough time has elapsed for the development of either a monoclimate or a polyclimate forest, unless we are prepared to call any group of plants a climate, regardless of how ephemeral the association may prove to be. An ecological study of the Ozark forest must not overlook the short time which has elapsed since the area was either "sterile" or grassland.

HISTORICAL ACCOUNT OF THE OZARKS VEGETATIONAL ASPECT

The Ozark Highlands of Missouri is unique as one of the oldest land-masses of the North American continent. Here on a land of archaic plains, deeply dissected by rivers entrenched in ancient meandering courses, erosion has carved in high relief, the land of rugged beauty we know today. It is only fitting, then, that rooted into a land having such a singular geologic background we find a flora equally interesting. In the Cambrian and Ordovician rocks, which comprise the greater part of the Ozark highlands, the history of the area may be read, and there is little evidence today of the varied floral aspects presented by Ozarkia in times past. However, turning to the diaries and journals kept by early explorers and travelers there is considerable evidence that the vegetational aspect of Ozarkia has never been static, and the rich hardwood forests which today add so much to the beauty of the Ozark mountain region are of relatively recent development.

The early Spanish and French discoverers in the Mississippi and Missouri River Valleys give us the first accounts of the early aspects of the Ozark region. Bearing in mind that the primary interest of those adventuring soldier explorers was the discovery of land rich in precious metals for the crown and that they were interested more in fruits and edible herbs, wood for fuel, and the construction of boats and simple fortifications than in botany, it is understandable that only a scant record was made of the native vegetation. The general structure of the Ozarks is of Cambrian and Ordovician rocks of more or less uniform composition, and a general habit for the whole region may be assumed on the basis of material reported from relatively localized areas, except where special modifications due to soil and water are noted.

The Ozark area was discovered by Ferdinand DeSoto in 1541 and included in the region then known as Florida. Houck (1908) believes DeSoto entered Missouri from Arkansas and, because of the numerous swamps of the region, took advantage of the highland now known as Crowley's Ridge. It was from here that the hearts of the travel-weary soldiers of DeSoto were lightened by the sight of the village of the Casquins. We are told that the fields upon the rich alluvial bottoms were planted in maize, and the pecan, plums, and mulberry trees were abundant. That

it was possible to see the distant village can only have meant that the soldiers were in an open, very park-like country unlike the dense forest of hardwoods that cloak this region today.

In the narrative of Garcilasso de la Vega, chronicler of the DeSoto expedition, we learn that DeSoto sent two of his men, accompanied by Indian guides, forty leagues to the north seeking salt and precious metals. The men returned eleven days later laden with salt and copper, but spent and famished. They reported that the country, indicated by Houck to have been the highlands and headwaters of the St. Francis River, was sterile and thinly populated. Indians of that region informed them that the country farther north was almost uninhabited, and that the interior of the Ozarks was even more sterile. Leaving the land of the Casquins, DeSoto marched southwest into the bottoms of the Little River. Here the gentleman of Elvas, also a chronicler of the DeSoto expedition, tells us of a land "full of good meadows on the river," from which only recently a vast forest has been removed. Quitting the swampy lowlands country in tireless quest of gold, DeSoto and his men marched northward toward Caligoa, believed by Houck and supported by Nuttall and Schoolcraft to have been the elevated highlands between the Black and St. Francis rivers, and at that time a land devoid of timber where herds of buffalo roamed. In the swampy lowlands and on the loessial hills bordering the Mississippi River, a more park-like aspect prevailed, as indicated by Garcilasso's description of the country of the Casquins.

Coronado, in 1541, is believed to have reached the southwestern portion of Missouri (Houck, 1908). The prairie aspect is indicated there by his notation of a rolling grassland, well watered with many rivers, and Osage Indians hunting among the vast herds of buffalo.

After DeSoto and Coronado, a period of French explorations begins. Entering the Mississippi Valley from the Great Lakes Region and seeking a water route to the Vermillion or Indian Ocean, the explorers travelled chiefly in bark canoes upon the rivers, and acquired little knowledge of the interiors. Father Membre, accompanying LaSalle down the Mississippi in 1683, has pointed out that the groves were so open and unobstructed one could ride through them on horseback. But even in those early years the appearance of Ozarkia was changing rapidly. Joutel, writing of the vicinity of Saline Creek in 1687, says: "The country was full of hillocks, covered with Oak and Walnut trees, and an abundance of Plum trees . . ." (Houck, 1908). Already we see indications of the encroaching forest. However, the forest was still conspicuously park-like, and Father Vivier in 1750 writes:

Both banks of the Mississippi are bordered throughout the whole of its course by two strips of dense forests, the depth of which varies, more or less, from half a league to four leagues. Behind these forests the country is more elevated, and is intersected by plains and groves, wherein trees are almost as thinly scattered as in our public promenades. This is partly due to the fact that the savages set fire to the prairies toward the end of autumn, when the grass is dry; the fire spreads everywhere and destroys most of the young trees. This does not happen in places nearer the river, because the land being lower and consequently more watery the grass remains green longer and less susceptible to the attack of fire. (Houck, 1908).

As late as 1789 Forman was told by Captain Foucher, Spanish Commandant at New Madrid, that he could drive a coach-and-four through the open woods from New Madrid to St. Louis. It was inevitable that a resident population be attracted first to the eastern border of the Ozark region, and it was about 1704 that the first settlers made their home in the vicinity of Ste. Genevieve (Sauér, 1920). Here, conveniently located to Indian tribes and the fur trade, with an abundance of salt close at hand, and with the Arcadian abundance of the land, they had an easy existence. Trading in furs and mining for lead occupied most of their attention, but of this period we have only scattering impressions of the aspect of Ozarkia.

It was not until the cession of the Louisiana Territory to the United States in 1803 that any real consideration was paid to the resources of the area. Then, as in earlier years, an "open aspect" of the Ozarks predominated. The uplands in the interior were a rich grassland and supported numerous species of the "broad leaved" herbaceous plants. Numerous barrens were found in the dolomitic and porphyritic hills, and there the vegetation was sparse. At this time trees were, for the most part, found only at wide intervals bordering the water courses, in deeper and richer soils of the uplands as isolated specimens, or occasionally in small park-like groves. In a sketch of the Louisiana territory, Major Amos Stoddard, who had accepted the land in the name of the United States in 1803, writes: "The highlands are seldom so thickly covered with wood as to prevent the growth of grass. They exhibit more an appearance of extensive meadows than of rude and gloomy forests."

In 1819 Schoolcraft, who toured the Ozark region on foot studying the mine country, was also impressed with the openness of the area, and observed:

The general aspect of the country is sterile Respecting the botanical character of the mineral soil, it may be further observed that although it yields but few forest trees, and they are not of a vigorous growth, yet a botanist might find his labors well rewarded by the profusion of shrubs and wildflowers which are everywhere found on the barrens.

In regard to the region between Herculeaneum and the Meramec River, which today supports notable timbered lands, Schoolcraft (1819) noted:

Our road this day has lain across a sterile tract of country, consisting of a succession of hills of moderate elevation, covered chiefly by oaks and without underbrush. A tall, thick, and rank growth of wild grass, covers the whole country, in which the oaks are standing interspersed, like fruit trees in some well cultivated orchard, and giving to the scenery the most novel, pleasing, and picturesque appearance.

And this was a general condition, for he describes the country in the vicinity of Bourbon thus:

Our route this day has been over barrens and prairies, with occasional forests of oak, the soil poor, and covered with grass, and very little underbrush. As evening approached we entered the valley of the Merrimack, which we followed up for several miles, and encamped in a prairie near its source. Some good bottom lands are found on its banks, but the adjoining hills are stony and barren, covered with little timber and high grass. (Schoolcraft, 1821).

Bradbury, who traveled the Ozarks concurrently with Schoolcraft, wrote:

The general character of this country is that of prairie, with scattered trees and interspersed clumps The tract of country which contains the mines is very uneven, consisting of high narrow ridges, separated from each other by deep craggy glens; the ridges have a peculiarly bald and arid appearance (Bradbury, 1819).

The exploring expeditions sent out after the Louisiana Purchase were bound for the mountains, prairies, and deserts of the Far West and they give little first-hand information of the Ozark country. However, Dr. Baldwin, accompanying the Long Expedition as Botanist on its western explorations in 1820, has left some impressions of the country in the vicinity of St. Louis. Collecting plants in the region of the mouth of the Meramec River, Dr. Baldwin found a typical prairie flora, and noted: "The grassy plains to the west of St. Louis are ornamented with many beautifully flowering herbaceous plants . . . The borders of this plain begin to be overrun with a humble growth of Black-jack and Witch Hazel." (Baldwin, 1823).

Twenty years later we find the openness of the Ozarks still prevalent, as Davenport (1842) tells us: "There is no part of the globe, in a state of nature where greater extents of country can be traversed more easily, and in any direction, by carriages of any description." Featherstonhaugh (1844) describes the region near Herculaneum after climbing a rugged hill: ". . . at the top of which we found ourselves in extensive barrens containing straggling trees."

During a period of settlement in the Ozark area, indicated by Sauer to be about 1820-1850, we find indications of the forest slowly and surely encroaching upon the prairie grasses dominant for so long a time. Settlement and the reduction of prairie fires favored the development of a forest flora as Swallow (1859) points out:

The slopes and some of the highlands are covered with heavy forests of nearly all the trees found in the bottoms But a still larger part is sparsely timbered . . . : forming the beautiful oak openings. This stunted growth is not, however, due to the poverty of the soil, but to the fires which have annually overrun this country since the earliest dates of the Indian traditions.

Jewett (1866), reporting on the agriculture of Jefferson County, writes: "The country is entirely covered with timber, except where improved . . . the Oaks and Hickory predominating." Elsewhere woody growth was seen invading the prairies. Broadhead (1873) reports on Barton County: "The first signs of a growth of timber on the prairies is the appearance of small Persimmon bushes. They are common nearly everywhere"; and, "In southern Missouri open prairies are rare, but in their stead are occasional large tracts of barrens, or hilly districts covered with tall grass, on which are scattering stunted Oaks . . ." Sargent, in 1884, notes: "A gratifying improvement in the condition of the forest in the parts of the state first settled has followed the enactment of a fence law preventing the general ranging of stock through the timber land."

Toward the close of the nineteenth century we find growing concern over future timber supplies for extensive lumbering, and the widespread use of wooden ties for a rapidly expanding railroad system was making noticeable reductions upon a forest which was still somewhat open. However, Shepard (1898) reporting on the geology of Greene County writes:

It is a mistaken idea that the supply of timber in this region is decreasing; on the contrary it is largely increasing. Attention was first called to this fact by Mr. J. W. Blankinship who has given a great deal of study to the flora of the region. He learned from the testimony of old settlers that seventy years ago there was probably not one-half the timber in the country that there now is It has probably increased one-third within the last forty years.

When Henry Shaw first visited the area which is now the Missouri Botanical Garden in 1820, he observed that "for a distance of two miles no trees were growing . . . The prairie was grown over with a tall, natural grass." (Shaw, 1880).

Thus we see that the encroachment of forest upon the ancient prairies has been rapid indeed and that our forests as we know them today are of relatively recent origin. The barrens which were conspicuous in earlier times in their paucity of vegetation have remained as "islands" included within the forests, and are observed as botanical and geologic oddities.

PRESENT FOREST RESOURCES

King, Roberts, and Winters (1949) point out that "Missouri's forests are largely composed of immature stands" and that only 14 per cent of the "land bearing or capable of bearing commercial timber" supports stands of saw-timber value. In a summary they state that 43 per cent is in pole timber, 32 per cent in seedlings and saplings, and 12 per cent is poorly stocked. Thus, nearly 90 per cent of the commercial forest land is in immature stands. The saw-timber averages only 789 bd. ft. per acre; 5 per cent of the forest land supports 3,000 ft. per acre; and an additional 10 per cent, 2,000 ft. per acre. They also point out that one-third of the gross value is in cull trees and unmerchantable species. In addition, the net growth per acre is estimated at 38 bd. ft. in the Ozark region and reaches only 59 bd. ft. in the river-border region. They suggest that the commercial forest land might ultimately produce three times the present value of growth under good management.

The Ozarks as a forest region is disregarded by Cheyney (1942), and the species of trees growing there are included among those of the forests of the Lake states and of the Atlantic and the Gulf Coastal Plains. Apparently, the bd. ft.-production per acre is so low that logging has not developed to the magnitude found in other areas. Even today, it is a region from which much of the output of the saw-mill goes into specialized products. Logging is reported to have reached its peak in Missouri about 1900, when 1,169 saw-mills produced three-quarter billion board feet of lumber, and approximately three million cross-ties. From such figures it is apparent that within the space of fifty years most of the merchantable timber in the state was logged. At present, the net growth of the growing stock exceeds the cutting drain by only 1.8 per cent annually. At this rate, it would take 225 years to support five times the present volume of saw-timber. The logging industry revolves around a vast number of small mills operating seasonally. There is no evidence that the type of logging has changed greatly in the last fifty years. The backbone of the lumber industry at present is the 1,585 mills or 56 per cent of the total in the state, which produce 68 per cent of the total lumber. Many of these are under-powered and poorly equipped. Their annual cut ranges from 50,000 to 500,000 bd. ft. each, and there are only 45 mills which cut more than a million board feet annually.

The complete picture of the saw-milling operation in Missouri does not convey the impression that the Ozarks were once stocked with magnificent forests. Only fifty years have elapsed since saw-milling reached its peak, and less than 150 years since the first logging camps were established on the headwaters of the Gasconade River. Due to the transportation difficulties before the advent of the railroads and to an uncertain market, the earliest lumber operations largely served a local territory. These factors would have tended to conserve the resources in the early stages. Later, of course, improved transportation made the products of the Ozark saw-mills available throughout the Middle West. This would also have favored an increase in the annual cut which reached a peak 50 years ago and was not approached even during the favorable years of 1940 to 1946.

THE RED CEDAR

At one time the scarcity of fencing material was considered a handicap to the settlement of the western country. Since such huge quantities of cedar posts are available and are so generally used in fencing today, we may wonder what position the Red Cedar (*Juniperus virginiana*) occupied in the early forests. Stoddard (1812) found, "it in plenty on the banks of the Mississippi and some other rivers above the mouth of the Illinois." Brackenridge (1817) found it on the Meramec, St. Francis, Missouri, and the Mississippi—"some very large islands on the Missouri are covered with this tree." It is very likely, however, that the "cedar" of Brackenridge was the Bald Cypress (*Taxodium distichum*) and not the Red Cedar (*Juniperus virginiana*). Bradbury (1819) found it along the Gasconade and Missouri River bluffs and mentions "that the tops are crowned with Cedars." Swallow (1855) places its habitat as the "dry limestone bluffs." Broadhead (1874), writing of Madison County, said that "Cedar Creek contained some of the finest groves in the state." He also mentions that great quantities have been cut for fence posts from the vicinity of Leatherwood Creek and Gray's Mountain.

Between the time when fencing material was scarce to the time of Broadhead's observations, there are not many references to this tree. From this we might infer that the species was not nearly so conspicuous as it is today. It would have been impossible for it to have escaped the attention of Featherstonhaugh. Today *Juniperus virginiana* is one of the most common trees in the Ozarks, and on the northern edge it has taken over the role of pioneer and invader. It very often precedes the elm, persimmon, and sassafras trees which Swallow (1855) reported as "not common." The Red Cedar is quite shade-tolerant and will persist in grassland until a favorable opportunity for rapid growth arrives. It is one of the major competitors of old established trees. The seeds, voided by birds, germinate in all fence corners, open fields, and in the soil beneath the branches of any tree under which they happen to fall.

This vigorous encroachment on fields and timber land by the Red Cedar appears to result from the control of fires. There are few species of trees more susceptible to fire injury than this tree. The annual burning of fields and woods which was

so very common until just recently would have kept it within bounds. Beecher (1950) writes that the junipers (Red Cedars) were hardly known in Franklin County in 1900, and that when needed for Christmas decoration it was necessary to cross the Meramec River into Jefferson County to find suitable specimens. Today this species has gone north of the Missouri River and appears altogether too often on the grasslands in Callaway County. Unless burning is practiced, the Red Cedar has demonstrated that it can, in a short time, become the dominant tree in the entire Ozark region.

SOILS AND EROSION

Extraordinary efforts are being made throughout the country to prevent erosion and retain the topsoil. It is stated again and again that the early settlers "mined" the soil and then moved on to new land to repeat the process. However, travelers have left a description of the original Ozark soil, and it appears to have changed very little. Schoolcraft (1819), in his "Tour of the Mine Country," reported the "soil as a reddish coloured clay, stiff and hard, and full of fragments of flinty stone, quartz, and gravel: this extends to a depth of 10 to 20 feet, and is bottomed on limestone rock." Bradbury (1819), traveling through the Missouri Territory, noted that "the stratum immediately below the vegetable soil is almost universally a very tenacious clay and extremely well calculated to form a material for bricks." His prediction is borne out by the extensive clay-products industry which has developed through central and eastern Missouri. James (1823) described the Loutre and Grand prairies in Warren and Montgomery counties as having a soil which "was not very good; but mixed at the surface with so much vegetable matter, accumulated by the successive growth and decomposition of the yearly products, as to give it the aspect of fertility." This observation is especially interesting, since these counties are still predominantly grasslands.

Obviously there has never been a deep, rich topsoil capable of supporting an intensive kind of agriculture in the Ozarks. Nor, can any evidence be found to indicate that these soils ever approached typical forest soils—the podsolic soils of the north on which good forests are found. Rather these soils approach the Groot soils, the nut-structured Prairie-Forest soils (Wilde, 1946), or the "Lime Prairies" (Hilgard, 1906), described as a clay soil overlaying weathered limestone. Wilde points out that the transitional prairie soils present a picture of a struggle between grass and trees and that "this struggle does not end even when the forest canopy is closed over the prairie soil." He further states that the struggle "involves not only plants, but animals and lower organisms as well."

Although it appears that the Ozark soil has always been much like the soil we know today, erosion may have increased in the past few years, if we recall Seay's (1866) observation on the absence of ditches in Crawford County. Perhaps the "newness" of erosion as a possible factor in Ozark land use is best illustrated by the numerous earth mounds thrown up by the Mound Builders. Houck (1908) was able to locate 28,000 mounds in Missouri. These earthworks, laboriously con-

constructed by a prehistoric people, required the moving of millions of cubic yards of soil. To have succeeded in such a gigantic undertaking, each basket of soil carried to the top must have remained in place. The mounds could not have been built during a period of rapid erosion. The years during which they have been exposed to all weathering agencies is indicated by Houck, who states that the Indians found by the first white explorers did not recognize the mounds as their property nor did they use them or have any traditions concerning their origin. Stoddard (1812) says that they "have endured for centuries. The trees on their ramparts . . . indicate an age of more than four hundred years." Pustmueller (1950), describing Monks Mound, states that "most of the trees have grown large in recent years, for at one time it was nearly bare." Only lately have the members of the St. Louis Archaeological Society been concerned over the destructive action of erosion, although the mounds have been a part of the Ozark landscape (Walker and Adams, 1946) for centuries. Now, after eight centuries, Monks Mound, rising over 100 feet above the adjoining country, is being slowly destroyed by gullies.

FIRES

Few travellers have written as vividly about Ozark fires as Featherstonhaugh (1844), who measured the progress of a fire at a camp eight miles from the Current River. He mentions that hunters used fire to drive game, and that in consequence of camp fires being left burning, "many thousands of acres were burnt over." In approaching Little Rock he expressed concern lest he be caught crossing a valley in which a fire was raging. Certainly, these fires have been common in the whole region from the earliest times. Swallow (1859), in his report following a railroad survey, describes central and southwestern Missouri as "in large part sparsely timbered, forming the beautiful *oak-openings*. This stunted growth is not, however, due to the poverty of the soil, but to the fires which have annually overrun this country since the earliest dates of the Indian traditions." Annual burning would have given the grasses and herbaceous plants every advantage by destroying the woody plants as well as the seedlings. Featherstonhaugh expressed the opinion "of Mr. Jefferson and others that all prairies have been produced by the Indian practice of firing annually, and thus destroying the grown timber as well as inferior plants."

Fires are probably an extremely important factor in the maintenance of the openness of the country, and may have aided indirectly in the production of tremendous quantities of seeds and fruits. Later, as the country became populated and the settler had much more to lose, the practice of burning annually was frowned on. A fire advancing on a homestead, as described by Featherstonhaugh, could destroy the cabin, whatever stock of grain the settler had, and, by destroying his fences, leave the fields open to the roving game and cattle. Even today the burning of woods is carried on only in those "backwood" areas where a kind of subsistence farming exists.

Officials charged with fire control have long since learned that the native backwoodsman considers burning the woods his prerogative, and he cannot be convinced that he is doing harm. When apprehended he is able to offer only a few "lame" excuses; among them, he wishes "to increase the grass" or "destroy the insects." When we consider that these people, the direct descendants of the first white settlers, are almost inarticulate with strangers, and especially in a court of law, it may not seem so extraordinary that they are unable to convey their knowledge handed down through the years, of the openness of the timber and the grazing which was once available to cattle. Their insistence that they can "improve the grass" is not without foundation, since they alone have more than an academic connection with the past. There are no fires in the sections where farming has developed sufficient stability, and where there are only remote or no ancestral connections with the past.

Swallow (1859) clearly indicates that a reduction in fire would result in an increase in timber. Sauer, illustrating the early opinion that fires checked tree growth, quotes the refusal by the United States of a grant of land to raise timber, on the ground that "it is only necessary to keep out the fires to cover the prairies with timber by the operations of nature." Along the northern edge of the Ozarks, fire protection favors the woody plants to such an extent that fields are completely reseeded in just a few years. The American Elm (*Ulmus americana*), Red Cedar (*Juniperus virginiana*), Soft Maple (*Acer saccharinum*), and locally the persimmon (*Diospyros virginiana*), and sassafras (*Sassafras albidum*) are all invaders of abandoned fields which have been given fire protection. These species can maintain themselves after gaining a foothold, but can be seriously injured and set back by fires at any time in their early years. If fire is allowed to enter such a field the reduction in growth rate follows a pattern so frequently described in present-day conservation literature. It is noteworthy that the light-seeded trees are the invaders of open ground, and not the oaks whose heavier seeds are probably planted by the smaller animals. If the oaks were the dominant trees of the area, and they are so described by both Swallow and Featherstonhaugh, they would spread rather slowly from the parent trees. This would indicate that the invasion rate a century ago was very much slower than it is today where fruiting specimens of light-seeded trees can be found in every ditch row, and where protection from fire favors their rapid spread.

RAINFALL AND SALINES

The early travelers spoke very highly of the healthful Missouri climate, but it is not possible to learn from the Weather Bureau records whether there has been any major change in the last century and a half. The records of the St. Louis office go back to 1837, but they do not show any pattern in the distribution of rainfall. For instance, in November, 1865, not a drop of rain fell, while the maximum for November is 8.63 inches in 1847. December records show as little as .18 inches of rain and as much as 10.90 inches. July and August are usually

drier with a minimum of .25 inches for July and .07 inches for August. The maximum is 20.45 inches for August 1946 and 9.50 inches for July 1875. This wide variation in precipitation serves only to demonstrate the limited value of precipitation records in so far as plant growth is concerned, and all efforts to discover trends toward an improvement or deterioration in climate have been unsuccessful.

There must have been an appreciable increase in annual rainfall to have favored the explosive invasion of the grassland by the trees. Much less rainfall is needed to grow good grass than trees, and it is only necessary to observe the area 400 miles west of St. Louis to see a first-hand struggle between grass and trees for the available moisture. Raup (1937) is convinced that the prairies at one time extended as far east as the Hudson Valley.

If there has been a great increase in precipitation, it probably occurred just before the establishment of Spanish colonies in the Mississippi Valley. Of Marquette's description of the Mississippi in the vicinity of Grand Tower, Houck (1908) writes:

It is quite evident that Marquette here refers to the stretch of river about Grand Tower, although it does not exactly describe the present condition. But 225 years will effect great changes, and that the river has widened in that period and that some rocky obstacles have been washed away is also certain.

The seasons at that time appear to have become wetter. Since precipitation records are of no value in furnishing the needed information, it becomes necessary to rely on the early writers for proof. Featherstonhaugh (1844) wrote that "at one time voices could be heard across the Mississippi at St. Louis"—a far smaller stream than the Mississippi of today!

One of the important occupations of all settlers and travelers was the procurement of salt. From the time DeSoto sent some of his party north for this purpose until almost two centuries later, when Moses Austin (1797) reported that the salt works, "when extended, might furnish all the upper settlements on the Mississippi," the evaporation of salt was a major project. In 1799, the works on Saline Creek in Ste. Genevieve County, produced 956 bushels of salt. Daniel Boone operated a salt lick which became sufficiently famous to lend its name to a major highway west—Boone's Lick Road. The fastidious Featherstonhaugh often refused the rough fare made available to travelers because much of the salt in use was gathered with a spade from a "lick," and both the salt and the soil was added to the cooking. Schoolcraft reports a salt lick near the present site of Fenton and two salt-manufacturing operations nine miles from Herculaneum. He mentions another salt-lick in the Bellevue Valley, and he describes a buffalo lick called Bates' Lick covering about twelve acres and worn by game to a depth of ten or twelve feet.

Although modern industry has supplanted the old iron kettle and evaporating pans and now supplies a very high-grade salt, the "licks" have vanished. It would seem that there are only two possible causes for their disappearance: (1) The rainfall may have increased so much that the brackish water is being diluted, and

the water of today could not be used in the crude evaporating pans; (2) The growth of timber has greatly reduced the flow from springs, with the result that those which were used as sources of salt have now dried up or flow intermittently only during wet weather when the "salty" character would go undetected. The smaller springs, perhaps flowing seasonally, furnished the supply of salt for the "licks" used by both the game and the travelers.

It is well known that the maximum amount of percolation occurs on a good sod where run-off is reduced to a minimum, while a very appreciable part of the rainfall striking the forest cover is evaporated. Edward Clark, in a personal communication, expressed the thought that the disappearance of the salt licks might be partly due to increased precipitation. Wolff (1948), working in the drier climate of Oklahoma, has shown that restoration of grass cover increased the flow of springs which had been checked by the advancing timber line. In his work with "cedar brakes" on the Edwards Plateau he was able to restore intermittent springs to full-time flowage by removing the cedars from the watershed and re-seeding to grass.

It would seem that a climatic change tending toward increased precipitation has occurred in the Mississippi Valley and the near-by Ozark highlands. In a report on Crawford County, Seay (1866) states:

The valleys . . . are frequently wide, scarcely ever rocky, covered with grass or hazel, with a deep, loose, sandy soil, and generally no definite channel to them. The water, if it accumulates rapidly, washes over the whole ground, but hardly ever so as to do any serious damage; and [in] an ordinary wet spell the water never finds its way out, but sinks.

It would hardly seem necessary to point out that there are few if any valleys in Crawford County today that are not bisected by a drainage-way in the form of a fast eroding ditch. The salt "licks" have disappeared and the forest has invaded the grass land. The additional rainfall may have been all that was needed to support trees. It has been demonstrated (Wolff, 1948) that a tree cover reduces percolation and reduces the flow of springs, while a grass cover, checking run-off, favors percolation and ground storage of water.

SEED PRODUCTION

Assuming that the Ozark highland experienced less rainfall two centuries ago than today, the leaching of soluble plant food would have been reduced to a minimum. This would have assisted in maintaining fertility at a fairly high level, which could be expected to stimulate seed production. Foresters have long been familiar with the "good" seed years which follow a severe drought. Kraus and Kraybill (1918) have shown that fruit production is correlated with the carbohydrate-nitrogen ratio. Klebs (1918) points out that during a hot, dry summer there is an excess production of carbohydrates in relation to the nutrient salts. This "in turn increases the probability of flower formation." Heyward and Barnette (1934), investigating the effect of fires on the chemical composition of forest soils, stated:

The soils subjected to frequent fires were found to be consistently less acid, and to have higher percentages of replaceable calcium and total nitrogen. An indication was found that these burned soils were also characterized by larger quantities of organic matter as judged by loss on ignition.

The above investigations would serve to show the seed production potential of the Ozark area. With the trees widely scattered, a reduced precipitation, a minimum of leaching—all factors favoring flower formation—the stage was set for the production of heavy seed crops. That seed production was very heavy is convincingly shown in the early records. Audubon (Wilson and Bonapart, 1831) observing a flight of Passenger Pigeons, estimated that they consumed more than 17 million bushels of grain daily.

In 1700 Father Gravier (Houck, 1908) killed two bears in Scott County and saw fifty more cross the Mississippi River during one day. In the first statistical report of the Spanish settlement at St. Louis and Ste. Genevieve, Piernas (Houck, 1908), in 1772, listed 905 packs of furs shipped to New Orleans. These few citations, among many, indicate that the game "carrying capacity" of the region was tremendous. It follows, then, that the production of food must have been in keeping with the needs of the game, also that a vast assortment of food was available. Few of these game birds and animals can be found in the wooded Ozarks today. Not even the turkey, when given full protection, has staged a comeback.

Even though the Ozark woodland is rated as "understocked," we find trees growing so close together that very few individuals produce a crop of seed. The plum thickets at the edge of the woodlot and some of the smaller shrubby plants may seed annually, but the heavy production of mast on which the pioneers fattened their hogs is a thing of the past. Only those oaks which are growing as isolated individuals bear seed with any degree of regularity. Lawn trees and scattered oaks near the Arboretum nursery mature seed quite regularly, some individuals bearing heavy crops in alternate years. Many oaks in the forested areas have not produced seed in ten years, although they have been carefully watched since seed collections were needed to complete certain taxonomic work. Most of the trees submerged in the Ozark forest bear very infrequently, and some individuals apparently never set fruit. This would appear to be in contrast to the behavior of these same species a century or more ago. In a region of reduced rainfall and no leaching, one would expect a favorable balance of carbohydrate to nitrogen. Annual burning would have made plant food readily available. Widely spaced trees would have produced a maximum crop of fruit.

Tree fruits were not the only source of food. Many of the larger animals grazed as much as they browsed on the trees, or pawed the forest floor for acorns as do the deer today. This would suggest that the grassland contained a vast variety of species other than the Gramineae. Probably many of these were legumes stimulated by the same conditions which produced heavy "mast" yields from the scattered trees which were the early forests.

BEES

Native flower pollinators in the form of Bumble and Solitary bees of the genus *Megachile*, *Nomia*, *Osmia*, *Andrena*, and *Bombus* must have been present from the earliest times until destroyed by modern agriculture. However, Bradbury (1819) reports that the Honey Bee (*Apis mellifera*) crossed the Mississippi River in 1797 and moved westward 600 miles in the succeeding fourteen years. According to him, this "extraordinary progress in these parts is probably owing to a portion of the country being prairie, therefore yielding a succession of flowers during the whole summer which is not the case in forests." He points out that the Indian believed that when the Honey Bee appeared, the white man was not far behind.

The flora of the prairie must have contained many kinds of plants other than the grasses to have favored the astonishing increase and progress of the bee. Grass alone would not have supported the bee, nor would a forested region have furnished more than suitable colony sites. The vast quantities of game, both animals and birds, indicate that there was a heavy production of fruits and seeds. Modern beekeeping depends very largely upon the legumes as a source of nectar. To have produced the vast quantities of high protein foods required by the game, the country could not have been heavily forested, and the legumes must have made up a very appreciable part of the flora.

HISTORIC FLORA

Much has been written of the early vegetational aspects of the Ozark area, but there is only a scant record of specific plant material. However, the material available substantiates the vegetational aspect recorded of that time. For earliest records we must lean heavily upon Schoolcraft (1819, 1821) and Bradbury (1817) whose interests in natural history enabled them to record many valuable observations. Following them, the botanists Nuttall, Baldwin, and James, attached to westbound exploring parties, have left valuable notes on this early flora. However, as their route of travel lay along the Missouri River, they recorded little of the interior of the Ozarks. Tracy (1886) wrote the first flora of Missouri but admitted that, due to difficulties of travel and lack of sufficient field material, he had not included all the plants which probably grew in Missouri.

Naturally the attentions of the first travelers were attracted to the arboreal flora, for in a region of extensive prairies the presence or absence of trees for fuel and lumber was a deciding factor in the settlement of the region. Stoddard (1812) pointed out that the city of St. Louis may never grow to the west because the expanse of prairie there did not provide enough wood for fuel and fencing. Although the composition of the forest flora has not changed to any great extent, change is noted in a greater number of trees. Early travelers found nut-bearing trees and hardwoods on the ridges and prairies where the heavy growth disfavored the light-seeded trees. In the lowlands, rich alluvium and inundation permitted the growth of light-seeded trees. Bradbury (1817) found:

On the summits of the ridges, the timber is generally red cedar; on the prairie, post oak, black-jack oak, black walnut and shell bark hickory. The alluvion of the rivers contains a great variety, of which the principal are cotton wood, sycamore, over-cup oak, nettle tree, hoop ash, honey locust, black locust, coffee tree, pecan, and many of the trees common in the states east of the Alleghanies.

Stoddard (1812) found the Sugar Maple abundant near Cape Girardeau and the people making large quantities of sugar from the trees. He observed persimmon, mulberry, chestnut oak, iron wood, and crabapple growing on the "high ground" and noted: "Common to both the high and low grounds are sugar trees in abundance, several kinds of walnuts, several kinds of hackberry, cherry, buckeye, black and honey locust, three kinds of elm, gum tree, lyn, sassafras, nine bark, spice and leatherwood, two kinds of ash, and the coffee tree."

All the early settlers agreed that the Post Oak (*Quercus stellata*) was the most common tree scattered about the prairies. Schoolcraft (1819) writes of the Post Oak: "They are seldom found to grow higher than 30 feet, and 40 is the highest, seldom exceed a foot in diameter, and stand scattering." The Black-Jack and Shingle Oak also seem to have been common trees of the uplands.

Wild plums in thickets were common and prized for their fruit, as Brackenridge (1817) noted:

Amongst the wild fruits of Louisiana, the plum has been celebrated . . . there is none more interesting than the prairie plum, *Prunus Chickasa* [probably today our *Prunus angustifolia*], which literally covers tracts of ground of many acres in extent, and produces fruit so abundantly as to bend down to the earth with its weight.

Frequent references to the crabapple and hawthorns are to be found. As late as 1908 Sargent found the Ozark region a rich field in which to work as he monographed the genus *Crataegus*. These plants are not so conspicuous today and the recent invasion of the Red Cedar may be a factor in the failure of this genus so susceptible to the cedar rusts.

Wild grapes were common everywhere, and the vines were far larger than any we know today. Swallow (1859) measured vines from 22 to 27 inches in circumference, and 55 to 120 feet in length. Bradbury (1817) found a vine, near the Meramec River, 37 inches in circumference.

The rich prairie flora drew little comment from the earliest travelers. Schoolcraft (1819), however, remarks: ". . . a botanist might find his labours well rewarded by the profusion of shrubs and wild flowers which are everywhere found on the barrens." He was impressed with "sensitive brier," probably *Schrankia Nuttalli*, and mentions the peterswort, upland dock, and smartweed. Bradbury's list of plants found in the lead mine country included 75 species (Bradbury, 1817), and Thomas Nuttall was introducing "interesting plants" to Fraser's Nursery out of the Upper Louisiana Territory in 1813. Baldwin's (1823) notes are among the earliest specific references to the flora of the region, and he collected near the mouth of the Meramec: "*Rudbeckia hirta*, and *R. purpurea*, a small white flowering species of *Houstonia*, *Galium tinctorium*, *Smyrnum aureum*, a Phlox, a new species of *Potentilla*, a *Conyza*, the *Trifolium reflexum*, . . . *Campanula*

perfoliata, Diospyros virginiana, Rhus glabra, and many others." On the grassy plains west of St. Louis Dr. Baldwin observed "Aristolochia Siphon, Symplocos spectabile, Lilium catesbeiana, Bartsia coccinea, Triosteum perfoliatum, Cistus canadensis, Clematis viorna, and Tradescantia virginica." A notable feature of these early lists of plants is the consistent inclusion of the Leguminosae. Considering the great abundance of wildlife dependent on plants of this family for food, and the rapidity with which the Honey Bee spread, it is believed that the legumes were an important constituent of the early prairie flora, as they are today in most successful range growths.

Swampy lowlands of the southern Ozarks supported the impenetrable "brakes" of the giant cane (*Arundinaria macrosperma*), popular retreat of game of all sorts. Featherstonhaugh found it to be one of the favored haunts of the black bear. The settlers generally thought that the tender new spring shoots of the cane formed a superior pasture for livestock. (Schoolcraft, 1821; Featherstonhaugh, 1844). The cane has a very limited distribution today.

The joint-reed or rush (*Equisetum hyemale*) was common in the more northern parts of the Ozarks. Bradbury (1817) observed of it:

The rushes, *Equisetum hyemale*, were so thick and tall that it was both painful and difficult to walk along, even at a very slow pace the rushes are valuable, affording to the first settler winter food for his cattle for several years, after which they perish, being destroyed if fed on during the winter.

The tall, lush grasses of the prairies were impressive to all the travelers. Schoolcraft described them as "often as tall as a man on a horse," yet we find few records of their identity. Tracy (1886) wrote: "When the state was organized, our hills and prairies produced an abundant growth of buffalo grass which soon gave place to the blue joint which is, in turn, being driven out by the more valuable blue grass." It is significant that the buffalo grass is not listed in Tracy's flora, though C. S. Jeffries (1888), in a letter to Dr. G. Hardeman of Gray Summit, states that it was common in the area about 1876. Broadhead (1873) points out that the blue grass "grew well after the prairies have been grazed down."

GAME BIRDS AND ANIMALS

The open and park-like aspect of the Ozark region was further evidenced by the great herds of buffalo, elk, deer, and the flocks of turkeys, grouse and quails which the area supported. Certainly this was an important factor in the early settlement of the region, for nowhere in the middle-western country was a human existence made easier than here in the abundance of game, wild fruits, and clear springs and streams. These habitants of a prairie or park-like region bear vivid testimony of its high virginal fertility and productivity—a striking contrast to the low-carrying capacity we experience today.

That the wildlife was one of the dominant features of this region is indicated in some of the earliest writings. Garcilasso (Houck, 1908), recording the DeSoto expedition in 1541, tells us that in the Ozark country the buffalo were so numerous that the Indians did not cultivate corn but rather lived upon game. Con-

sidering the crude hunting arms of that time, game must have been abundant. Father Membre, accompanying LaSalle, wrote of this area: "The fields are full of all kinds of game, wild cattle, stags, does, deer, bears, turkeys, partridges, parrots, quails, woodcock, wild pigeons, and ringdoves." (Houck, 1908). In 1710 Father Vivier writes of the game, "the plains and forests contain wild cattle, which are found in herds; deer, elk, and bear Nowhere is game more abundant; from mid-October to the end of March the people live almost entirely on game, especially on wild ox and deer." (Houck, 1908). The "fields" of Father Membre, and the "plains" of Father Vivier clearly reflect the close relation of these vast animal numbers to the prairie habitat.

The very important part that trade in furs played in the economics of the early colonies may further illustrate the ease with which pelts were secured. Piernas, in his first and third Detailed Statistical Reports for St. Louis and Ste. Genevieve, reported 914 packs of furs in 1772, and 2,888 packs in 1774, sent to the capital, then at New Orleans. (Houck, 1908). Nor was game pursued for furs alone; much of the meat was "salted down" in the centers of large canoes, then known as "pettyaugers," hollowed from large cottonwood trees and often 50 feet long. Much meat was supplied to New Orleans in this manner (Houck, 1908). Birds, too, were present in overwhelming abundance. Bossu traveled in the neighborhood of the St. Francis River in 1764 (Houck, 1908) and found it difficult to sleep at night on account of the noise made by the great numbers of ducks, geese, swans, and cranes in these marshy areas. Perhaps no wildlife spectacle has ever equalled the prodigious numbers of the passenger pigeon described by Bossu as often eclipsing the sun. Audubon reckoned the number of passenger pigeons in one flock to be 1,115,136,000 (Wilson and Bonapart, 1831). Featherstonhaugh (1844) remarks about the ". . . whirring and croaking of tens of thousands of cranes . . ." on a sandbar in the Mississippi River near Herculanum. Townsend (1839), traveling westward toward the Rocky Mountains in 1834, noticed on the prairies near St. Charles, ". . . thousands of golden plovers; the ground was often literally covered with them for acres."

With an apparently unending supply of game on every hand it was inevitable that much needless waste and slaughter of animals and birds took place. Indeed, the effects were noticed at an early date. Houck reports that the reduction of game in lower Louisiana was conspicuous as early as 1750. This condition became general as the area became more populated with settlers. James (1823) wrote of his journey across the prairie west of St. Louis in 1820: "The elk, the deer, and the bison, the indigenous inhabitants of these delightful meadows, had long since been driven away by the incursions of the white settlers . . ." Audubon (Audubon & Bachman, 1851), in his travels up the Missouri River in 1843, did not come upon the elk and buffalo until he was a great distance up the river. The settlers and the trader-trappers have always been pointed out as the cause of this great waste. Much of this opinion is doubtless justified. However, in the light of the

current importance given to habitat in relation to animal populations, cannot similar principles be applied, in part, to the great historic reductions of wildlife? Vegetational aspect is the direct expression of geo-, climato-, and bio-relations, and conspicuous changes in floral aspect necessarily are the index of alteration of the habitat. We have noted already that the encroachment of white settlements upon the prairie lands was concurrently accompanied by the reduction of annual burning of the prairies which permitted the establishment of forest trees. A general reduction in fertility and productivity of principal game food sources has also been pointed out and together present such marked changes in the prairie habitat as to reduce seriously the carrying capacity of the area. Reduced in numbers by a decadent habitat, the extinction of major game animals and birds by an ever-increasing settler population was inevitable.

DISCUSSION

An attempt to apply conservation measures of any sort to the Ozarks must take into account that the transition from grassland to trees has been achieved in less than a century and a half. We cannot hope to develop a Bunyanesque kind of forestry in the region so recently invaded by trees. The failure to recognize the non-forest character of the area can only result, as Wilde (1946) indicates, in "a struggle that does not end even when the forest canopy is closed over the prairie soil." It is possible that many of our epidemic tree diseases may stem directly from their growing on a prairie and not a forest soil.

Forestry in the Ozarks can look forward to a multiplicity of problems until adequate time for trial-and-error selection points the way to dependable practices. The successful forestry project will be one which recognizes the fluid conditions prevailing, and is geared to profit by each and every advantage—no matter how unorthodox.

Laws have been enacted which make the firing of timber a criminal action. Fire, perhaps more than any other factor, maintained the prairie and park-like aspect of the Ozarks. But to be effective, the fire season must be long and dry. An increase in precipitation would lessen the effectiveness of fire, and the advancing tree line would suffer fewer disastrous burns. With the advent of white settlements, more and more portions of the area were protected from fire and these in turn furnished a haven for the advancing woodland. During every step of the invasion an increase in precipitation served to reduce the incidence and the damage which fire might cause.

The native backwoodsman (derisively called "ridge runners," "brush apes," etc.), who sets the woods ablaze, is a direct descendant of the first white settler. Without holding a brief for the woods-burner, we may well ask some questions. Is it wise to attempt commercial forestry in an area that averages less than 800 bd. ft. per acre, and when only 10 per cent of the forest supports 2,000 bd. ft. per acre—especially when at least one-third of this forest is in cull trees and trees of non-commercial species? Perhaps a large part of the Ozarks should remain in grass.

The earth works of the Mound Builders have demonstrated the absence of erosion through as much as eight centuries. They were reported at first as almost without trees, then supporting trees, and now in serious danger from erosion. The rainfall which was adequate for grass has increased to the point required by trees. Conservation programs of any character, whether engineering works designed to control floods, efforts to increase game, or simply to farm on a more even keel, cannot ignore the fact that the Ozarks are becoming milder and wetter. No flood-control project can succeed if it does not recognize this climatic change. Major floods in the Mississippi River occur with increasing regularity. The river at St. Louis is much wider than a century ago, and it may be significant that the spring floods in 1950 occurred on a north-to-south line from the Dakotas to Oklahoma. The loss of life and the property damage were aggravated by the fact that this area, without a history of heavy precipitation, was completely unprepared for the heavy rainfall.

An ecological study has shown clearly that the Ozark flora is immature, with the observed associations changing quite rapidly. In addition, the historical accounts of the vegetational character of the area bear out the contention that this is a young and vigorous flora not easily classified. Perhaps many species have disappeared, but one, the Red Cedar, has become more conspicuous by its aggressive pioneering in old fields.

The encroaching forest sounded the death knell of the big game and the game birds. Regardless of hunting pressure, the habitat had deteriorated so rapidly that the herds of game and flocks of birds were doomed. Gun pressure admittedly has increased from the day of the first white settlement. The hunter appeared on the scene and added just the necessary weight to force the game from a habitat which was rapidly becoming untenable. Game management, whether aimed at the increase of deer or the improvement of turkey or quail range, will always be confronted with the present instability of the Ozark weather as expressed by its effect on the vegetational cover. The "Aux Arcs" Mountains, once the habitat of buffalo, elk, and bear, cannot now support turkey under complete protection. A completely stocked forest of pole timber, which makes up 85 per cent of the forest area, is not a habitat for big game or game birds. From a mechanical standpoint, it isn't suitable even for buck deer; a buck with a trophy head will range in the pole timber only under fear and compulsion.

SUMMARY

An imposing list of writings, dating from the earliest travelers, clearly shows the predominance of grass in the Ozark landscape. Featherstonhaugh traveled by horse and buggy from St. Louis to Hot Springs, Arkansas, and the border of Mexico (now Texas). Today such a trip would be impossible except over established highways.

Insufficient time has elapsed to permit any plant association to be termed a climax.

A study of forest resources indicates that today's lumber production, in a favorable market, is far less than the peak which was reached in 1900. Eighty-five per cent of the commercial forest land is classified as "immature," and there is little likelihood of an increase in production in the foreseeable future.

Although very little information is available from Weather Bureau records, some pertinent observations are included which indicate that the Ozarks today enjoy a much milder and wetter climate. The disappearance of salt licks is deemed of considerable significance.

Apparently all factors favoring heavy seed production were present—heavy seed production is not of common occurrence today.

Sufficient information has been gathered to show the extremely important role of fire in the perpetuation of the grassland at the expense of the trees. As early as 1830 the United States Government recognized that the control of fires would clothe the prairies with trees.

The Red Cedar (*Juniperus virginiana*) has shown itself to be a most aggressive invader of the grassland and run-down fields. The beginning of its explosive invasion coincides roughly with reduced burning as a result of an increased population.

Bradbury's observations concerning the Honey Bee leaves little doubt of the open aspect of the country, with the legumes occupying an important position in the flora.

The tremendous quantity of game, easily exceeding that of the domestic cattle and fowl of today, indicates the vast amount of food which was available.

Typical podsolized soils, deemed to be characteristic of forest areas, are unknown in the Ozarks.

Soil erosion, rated as the worst enemy of fertility in the Ozarks, has only recently become important. Ninety years ago the fields in Crawford County were without gulleys. The Indian Mounds stood for centuries before showing signs of erosion.

ACKNOWLEDGMENTS

The authors wish to express their sincere appreciation to Mr. Charles Van Ravenswaay, Director, and the library staff, of the Missouri Historical Society, through whose efforts many important historical volumes were made available; to Mr. Trifon von Schrenk from whose library the authors have gained much valuable information; and to the library staff of the Missouri Botanical Garden for their kind and untiring assistance.

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THE CHANGING FOREST FLORA OF THE OZARKS

AUGUST P. BEILMANN* AND LOUIS G. BRENNER**

In this work the first time-lapse study on the forest flora of the northern Ozarks is reported. Brenner (1942) has shown the influence of the soils and the underlying rock strata upon the forest flora within a portion of the area covered, but the present study includes additional plant habitats and may be more representative. Recently the current associations were compared with those of an earlier map (Anderson, 1938), and the observed changes are here recorded.

GEOLOGY OF THE AREA

The area under discussion consists of about 650 acres in the Arboretum of the Missouri Botanical Garden at Gray Summit, Franklin County, R. 2 E., T. 43 N., Mo. It is a rectangular area lying within the rugged hills bordering the Meramec River, in the northern limits of the Ozark uplift, a region of dolomitic limestones weathered into a topography of moderate relief. A correlation of the logs from deep wells on the area has placed the underlying rocks in the Jefferson City, Cotter, and Powell formations of the Canadian Series, in the lower Ordovician Period (fig. 1.).

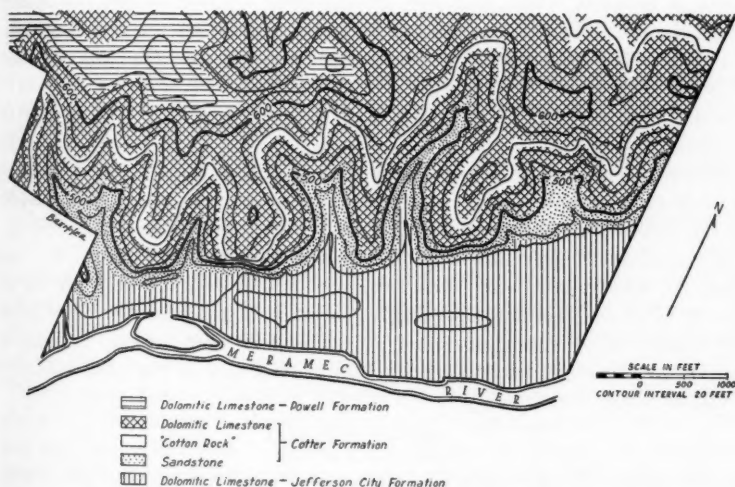


Fig. 1. The rocks underlying the Forest Preserve of the Arboretum.

Jefferson City Formation.—This formation forms the lowest outcrop to be found in the area, and is represented by a phase of dense gray-brown, oolitic, dolomitic limestone. This stratum outcrops at comparatively low elevations, and the

* Manager, Missouri Botanical Garden Arboretum.

** Assistant Manager, Missouri Botanical Garden Arboretum.

greater portions of it are covered with talus debris, considered to have only a small influence on the forest cover.

Cotter Formation.—The Cotter, lying unconformably upon the Jefferson City formation, is composed primarily of dolomitic limestones with sandstone phases of one to several feet in thickness, and thin shale lenses. The base of this formation is a gray-brown sandstone, 37 feet in thickness, and of interest because several perennial springs have their origin in this stratum. The sandstone is succeeded by a phase of dense, massive, slightly dolomitic limestone, 34 feet in thickness. The remaining 91 feet is composed of succeeding strata of medium-grained, loosely cemented sandstones; dense, oolitic, slightly dolomitic limestones; and relatively thin strata of pure dolomite, locally known as "cotton rock." In chemical content (a double carbonate of magnesium and calcium), in high porosity, and in degree of fractibility, the cotton rock may have a more direct influence upon the flora than any other stratum. The occurrence and distribution of glade floras have been shown to be directly related to these cotton-rock strata (Erickson, Brenner, Wraight, 1942).

Powell Formation.—The Powell is represented by somewhat thinly bedded strata of limestone, chert, dolomite, and sandstone. There are but few outcroppings, since the formation is almost completely overlain by the mantle of Union Silt Loam. The predominance of cotton rocks which permit the rapid percolation of water creates a "dry" appearance in the forest during most of the growing season. The ease with which water moves through these rocks is shown by the numerous springs, and by the great amount of seepage water to be found in the valleys in wet seasons. This rapid percolation of ground water does not encourage the deep penetration of tree roots into the rocks in search of water. The influence of the rocks is further reflected in the slow growth of the trees. The dolomitic rocks, because of their slow rate of decomposition (Hilgard, 1910; Lutz and Chandler, 1947), offer only small quantities of the minerals necessary for the growth of plants. Feeding roots seem to be concentrated primarily in the shallow soil mantle, where the decomposing organic matter offers greater quantities of nutrients. The effect of these two factors is evidenced in the glades which are devoid of forest trees.

SOILS OF THE AREA

The rocks, high relief, and the various exposures and angles of slopes, together with the pattern of land use, present a complexity of factors reflected in an equally complex "soil picture." Based on local peculiarities, the soils are divisible into two major groups: residual and alluvial. Because of the "upland" nature of the area, the alluvial soils are of relatively little importance and will be treated only briefly (fig. 2).

Union Silt Loam.—The Union Silt Loam represents the most important soil group by reason of its greater areal extent and its ability to support the better timber types at considerably faster growth rates. The soil is a brown to grayish-

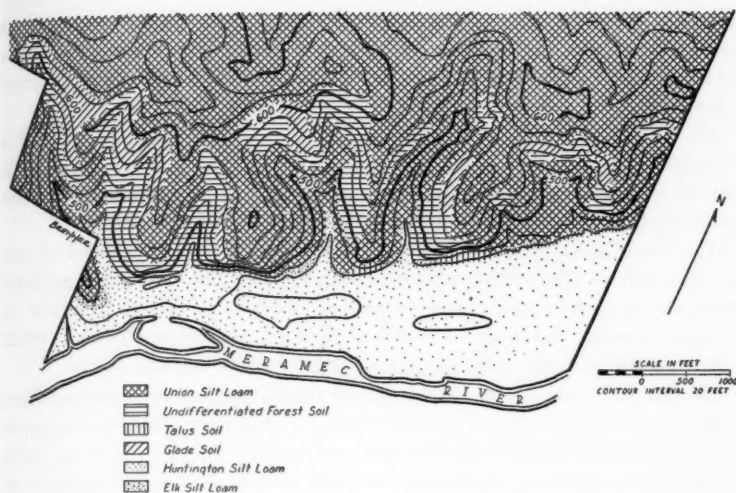


Fig. 2. Principal soil types of the Forest Preserve of the Arboretum.

brown, mellow silt loam, 6–8 inches deep, grading into a light brown or yellowish-brown, friable, silty clay of crumb-like structure, with a nut-like subsoil at greater depths. The fine silty nature of this soil and its great angle of slope make it an easy prey to erosion, which, however, can be controlled by planned forest management.

The Union Silt Loam in its typical form is apparent as the mantle covering the ridges. On some steeper slopes and small localized areas the soil is of a cherty nature and should be classed as Clarksville Stony Loam. However, because of the localized nature of this cherty soil and the history of land use of the area, the authors believe that it represents subsoil of the Union Silt Loam, exposed through erosion induced by early land use.

Rough Stony Land.—Extensive areas of the Arboretum have a soil generally referred to in soil surveys as Rough Stony Land (Vanatta and Lewis, 1911). The forest types found here have suggested the advisability of further division of this soil into four subtypes based upon site and mode of origin: Undifferentiated Forest Soil, Talus Soil, Glade Soil, and Alluvial Soil. The group is represented by soils which, because of direction and steepness of slope, have been retarded in development. Shallow, rocky, and of high organic content, they are entirely without distinguishable horizons.

The Undifferentiated Forest Soil is found chiefly on south and western hill-sides, and may be from a fraction of an inch to several inches in depth. The soil mantle lies immediately upon the bed rock, has a high organic content, and contains an abundance of rock fragments. Exposure of these slopes to sere late sum-

mer winds has discouraged herbaceous vegetation. This, together with the high angle of slope, has caused excessive erosion, resulting in an almost permanent juvenile state. The forest type listed as "Transitional" is almost entirely confined to this soil.

The Talus Soil is practically identical with the Undifferentiated Forest Soil in composition, but differs in its greater depth and in the constant movement of the mass through settling. These differences, along with a relatively low water table during drought, has discouraged the growth of good timber trees.

The Glade Soil represents a distinct type of shallow soil mantle derived from dolomitic rocks. The soil has a high organic content, but the underlying highly porous cotton rock of the Cotter Formation causes it to become extremely dry during the summer and extended periods of drought. Trees have found it difficult to invade glade areas and a flora typical of rocky prairies is found there.

Alluvial Soils.—As previously stated, the alluvial soils are of minor importance in this survey. Small areas of the "first bottom," assigned to the Huntington Silt Loam, are included as well as the Elk Silt Loam which forms the soil of the ancient Meramec River terraces. Although those soils are not of sufficient extent to influence the development of a distinct forest type, they are interesting additions to the complex picture of the soils of the area.

LAND USE

It has not been possible to determine exactly what use has been made of this land since 1850, when the first titles were granted. Certain portions show evidence of early timber cutting, at least for local use, and certainly quantities of firewood were also cut. Some hilltops have been clear-cut with the expectation of farming. All the area must have been heavily pastured by open-range cattle. In more recent years more intense utilization followed the fencing of pastures and the change from open-range conditions. It is not possible to furnish dates at which certain areas were pastured or cut over. On the whole, the history has been one of intense usage. Very few mature, sound trees can be found, and it is assumed that many have been cut. Usually, following such operations the land was grazed and quite frequently it was burned.

The extent and purpose of the timber cutting depended largely upon the topography of the area. The valleys and the more gently sloping hillsides were within the capacity of the equipment available to the early settlers. One area is reported to have been a sawmill site, and the condition of the adjacent timber indicates that it may have been clear-cut (indicated on fig. 3 as "Logged more than fifty years ago"). A number of older trees escaped the axe, probably because of their low value. Some of the high hill land may have been clear-cut "Less than fifty years ago." The areas so designated are without old trees, and much of the younger growth appears to have originated from stump sprouts. One fairly large valley was cultivated prior to 1925, when the area was acquired by the Missouri Botanical Garden, and a similar area is to be found near one of the ridge tops.

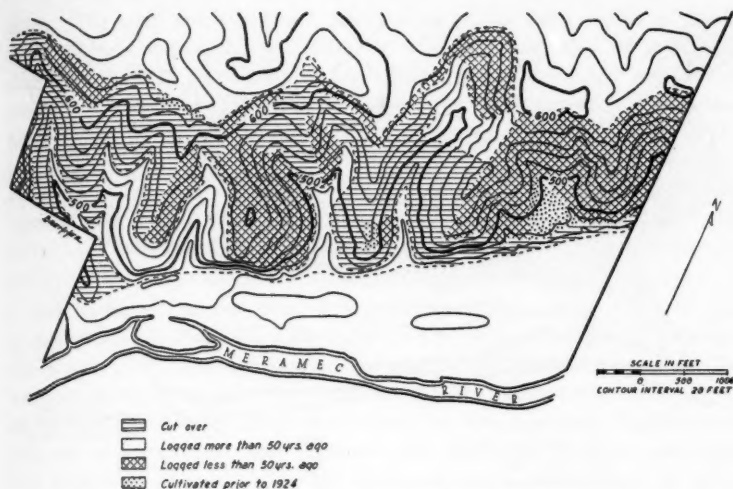


Fig. 3. History of land use of the Forest Preserve of the Arboretum.

The presence or absence of old trees may prove misleading when used as a measure of logging practices and land use. A few scattered old trees may indicate either that "selective" logging had been practiced—selective in the sense that the early settler cut certain trees for specific purposes—or merely that tremendous changes have occurred in the arboreal flora of the Ozarks in the last hundred years. Apparently, the Ozark forest today is more heavily stocked than it was a century ago, and the few relic trees to be found are those left from what was a park-like prairie (Schoolcraft, 1819) which seems to have been the outstanding characteristic of the region before 1850.

DEVELOPMENT OF TREE ASSOCIATIONS DURING A TEN YEAR PERIOD

Anderson's forest-tree classification (1938) has been modified to conform to present usage (fig. 4). The tree species involved in each association were covered by Brenner (1942). The extent and location of the present forest tree associations are shown in fig. 5.

Post Oak-Black Jack Oak (*Quercus stellata* - *Q. marilandica*) Association.—This association is limited to isolated stations on the ridges and to the Union Silt Loam, and appears to be highly unstable. The decadent nature of this association and the rapidity with which it has been absorbed by the more vigorous Oak-Hickory association indicate the speed with which the hardwood forests are encroaching upon the early prairie associations.

White Oak-Sugar Maple (*Quercus alba* - *Acer saccharum*) Association.—Distribution of the Sugar Maple appears to be controlled by the presence of old fruiting trees, and definite edaphic relations of this member of the association are not

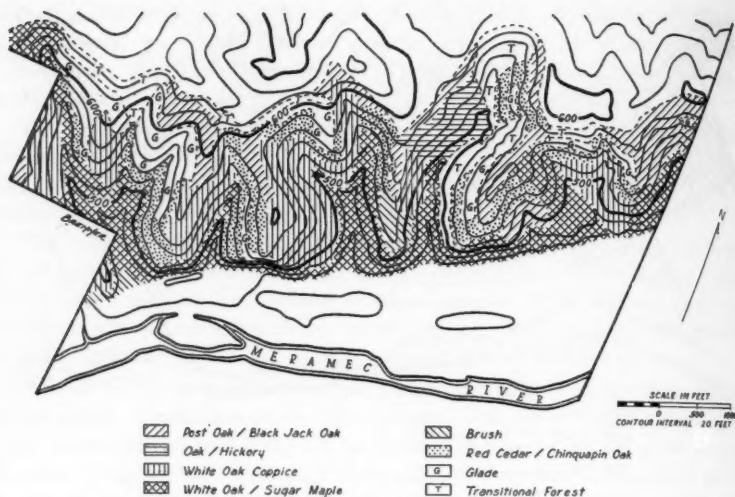


Fig. 4. Principal tree associations in 1938, Forest Preserve of the Arboretum.
(From an unpublished field survey in 1938 by Edgar Anderson.)

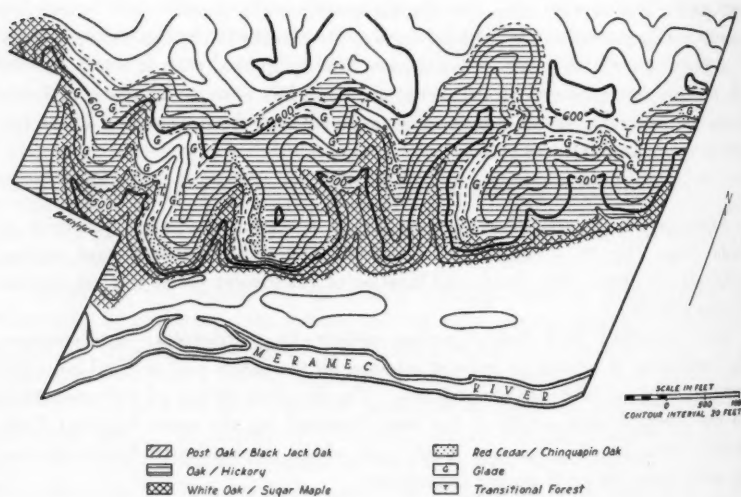


Fig. 5. Principal tree associations in 1948, Forest Preserve of the Arboretum.

shown. The rapid and widespread regeneration of the Sugar Maple in the deep moist valleys is apparently conditioned by the more favorable microclimate of those sites. In 1938 this association included several valleys where some selective cutting had been done in the last fifty years, but no clear-cutting for at least a hundred years. Such cutting and the resultant openings in the forest favored the rapid growth of the Sugar Maple. At present, however, it is losing its position as a codominant and may eventually disappear from this association. Above the valley floor the changes have been more rapid. The Sugar Maple in the White Oak-Sugar Maple Association of 1938 has been succeeded by hickory, and these areas are now classed as belonging to the Oak-Hickory Association.

Oak-Hickory (Quercus alba, Q. borealis, Q. stellata-Carya ovalis, C. ovata, C. tomentosa, C. Buckleyi) Association.—The high commercial value of these species, their rapid regeneration, and good annual increment make this forest association particularly important to foresters. The marked adaptability of these trees permits almost cosmopolitan distribution, for little preference is shown toward rock, soil, or direction of slope. However, the association has been most consistently mapped on areas of the Union Silt Loam where greater depth of soil and concurrent fertility have favored rapid growth and excellent regeneration. Perhaps no other tree association has had more continual exploitation. There is ample evidence that the trees have long been regarded as a source of firewood, rough lumber, and railroad ties, and such great use was made of them that in 1938 the Oak-Hickory Association was one of the least extensive in the area. However, it is becoming increasingly vigorous under the present system of land management and at present about 60 per cent of the area falls in this class. The Red Oak (*Quercus borealis*) and the important Shumard Red Oak (*Q. Shumardi*) are invading these associations and are becoming codominant with the White Oak.

White Oak Coppice (Quercus alba).—The White Oak Coppice is shown on the early map to cover about 20 per cent of the area. Nearly all of this is now included in the Oak-Hickory Association, with the Red Oak an important tree of the understory.

Red Cedar-Chinquapin Oak (Juniperus virginiana-Quercus Mublenbergii) Association.—This association is unique in being the only one of the area which is closely correlated with the underlying rock strata. On the accompanying maps (figs. 1, 4, 5) the Red Cedar-Chinquapin Oak Association is seen immediately bordering the cotton rock both above and below its extensive outcroppings on the western slopes. In this narrow belt, often a mere rod or two broad, the influence of the cotton rock still excludes other forest types. This association is shown to be more extensive on the map for 1938, since at that time accelerated erosion induced by earlier logging and pasturing only served to cause a more widespread effect of the conditions induced by the cotton rock. Rapid growth of the Red Cedar and its remarkable powers of regeneration have caused it to be exploited

greatly as a source of fence posts and telephone poles within the past fifty years. Today the association has a more limited distribution, and the Oak-Hickory and White Oak-Sugar Maple associations have apparently invaded much of its outlying portions.

Glade Association.—Here the inherent properties of the cotton rock in conjunction with a western exposure of slope have combined to form a critical zone for the growth of trees. Trees are conspicuously absent, an herbaceous, prairie-like flora prevailing.

Transitional Forest.—Because of its heterogenous composition and lack of aged specimens, the Transitional Forest is considered to be in a state of flux. Intensive exploitation of these sites through pasturing and logging has created a long-enduring juvenile state where the soil mantle is poorly defined. Comparison of the maps of early and present tree associations (figs. 4, 5), and the soil map (fig. 2) shows this association to be closely correlated with the Undifferentiated Forest Soil. Recent survey of the area shows the invasion of the Transitional Forest by Oak-Hickory and White Oak-Sugar Maple associations as the site matures and a deeper soil mantle protected by a layer of forest litter is developed.

Brush.—Several small areas classed as "Brush" in 1938 are now included in the White Oak-Sugar Maple Association. In 1938 those areas contained much sassafras (*Sassafras albidum*), elm (*Ulmus* sp.), and sumac (*Rbus copallina*), and were considered as not likely to persist. They are now stocked with some of the best young timber.

SUMMARY

Because studies in the natural succession of forest trees in the Ozark region of Missouri have been based largely upon site-to-site comparisons it is felt that this work, founded upon actual observations of the same area over a ten-year period, will give a better understanding of forest tree succession in the northern Ozarks region. Considerable attention has been given to both the rocks and the soils, since these have been observed to play important roles in the distribution of certain tree associations which may obtain only in similar areas. The history of land use of the area is reviewed, since the activities of man, in his pursuit of a livelihood in forestry and agriculture, may have altered the natural succession of forest trees.

This time-lapse study indicates a rapid invasion of valuable timber species such as Red Oak, White Oak, and White Hickory. The Black Jack Oak-Post Oak, and White Oak-Sugar Maple associations have been invaded by these vigorous species and will be dominated by them, indicating a future invaluable source of high-grade timber species in this area.

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HOW KENTUCKY BLUEGRASS GROWS*

ALFRED GORDON ETTER**

INTRODUCTION

Human cultures of widely varying origin have been treading sods of *Poa pratensis* for thousands of years, long before it became known as Kentucky bluegrass. Indifference to the plant's personality has been bred by this long familiarity, with the result that while bluegrass may often be thought of in terms of sod, turf, herbage, forage, or just plain grass, it is only rarely considered in terms of an individual plant. It is the purpose of this paper to describe in simple words what a bluegrass plant looks like and how it grows. In general, only that part of the organization and development will be considered which can be seen with the naked eye or low-power binocular microscope.

The importance of understanding the structure of a plant has become especially apparent in crop plants such as maize where solutions to practical problems—picking, detasseling, cultivating, spraying, cutting, and prevention of lodging—depend for their success on a knowledge of the manner in which the plant is put together. Anderson (1949) has stressed the need for this knowledge in maize and has raised many pertinent questions concerning the maize plant of the future. Bonnett (1935, 1940), in describing the development of the flowering head in barley and maize, has suggested the practical applications of such studies.

In spite of the ever-increasing number of grass farms and suburban homes with ample lawns, little effort has so far been made to relate developmental and morphological studies of forage and turf grasses to practical problems. Knowledge of the individual plant is fundamental to proper analysis of variation in any species, and consequently to the proper appreciation of its genetic possibilities; successful prediction and selection of strains to fit specific environmental conditions depend on such knowledge. Lawn and pasture species are constantly being subjected to management practices of various sorts. An understanding of the basic pattern of development of the plants involved is essential to any attempt to discern the effects of such treatment. Proper statistical planning and analysis of forage production and plot tests must necessarily be based on an appreciation of the variables involved in the normal growth processes of the individual plant. The widely varying and inconsistent results which are frequently obtained in pasture and turf research are probably partly due to the lack of information available on grass mechanics.

*The work reported in this paper was carried on while the author held a special fellowship under a bequest of the late Dr. Malvern B. Clopton. The field work was done at Brookhill Farm, Clarksville, Mo., Dr. Clopton's former estate, and the laboratory work in the Henry Shaw School of Botany of Washington University. It seemed a peculiarly appropriate project, since it concerned the bluegrass pastures at Brookhill which Dr. Clopton knew and loved so well. Grateful acknowledgment is made to Chancellor Compton and to members of the Brookhill Committee for making available this unusual opportunity and to the staff of the Doane Agricultural Service for friendly cooperation in the field. This investigation was submitted to the Board of Graduate Studies in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Washington University.

**New Mexico Military Institute, Roswell, N. M.

METHODS

Problems Involved.—Shortage of data devoted to growth of sod grasses may reflect the subtle difficulties involved in the measurement and description of their growth. Analysis of a wild population of grass is complicated by the fact that plants of different strains and different ages are all mixed up and growing together. Study of these grasses in the laboratory, greenhouse, or even the nursery plot, involves the introduction of artificial conditions which have been shown in several studies (Musgrave, 1940; Ahlgren, et al, 1945) to influence strongly the growth characteristics of the plants. Direct measurement of growing parts can scarcely be accomplished without damaging or removing protecting organs or soil, and consequent introduction of complicating factors. Indirect measurement of growth by examination of a number of plants in a developmental series is based on a number of assumptions which may be difficult to prove. (See van de Sande-Bakhuyzen, 1937).

Preliminary Studies.—Observations on bluegrass growth and morphology were made over a period of two years to provide a general understanding of the problem and the plant. Sodds were occasionally dug up, washed, and studied and diagrammed in detail. Special effort was made to discern seasonal trends. From these preliminary investigations sufficient familiarity with the plant was acquired to allow plot tests or laboratory experiments to be made on a small scale. Although the anticipated results were not always obtained, every new condition to which bluegrass was subjected yielded information of some sort. For example, in the course of measuring leaf growth on bluegrass grown in nutrient solutions, it became apparent that all plants of the same origin under the same conditions produced leaves at practically the same rate. Plants could thus be roughly arranged as to time of origin by referring to the number of leaves they bore. Specific periods in the life of a plant could be identified, since each plant that lived through the winter had one leaf shorter than all the rest of the leaves; also certain types of shoots were limited to the cool fall and winter period, while summer buds frequently remained dormant.

It soon became apparent that while the chief concern of the study was to shed light on problems of pasture and lawn, such places were not the best for studying bluegrass behaviour, for an excessive number of complicating factors were involved. Constant cutting maintains the plant in a vegetative condition and seasonal activity is not clearly defined. It was found that the most favorable place to study basic behaviour was in a relatively unproductive old meadow where mowing, treading, and fertilizing were minimum complications and where the grass could be expected to respond only to the strongest seasonal stimuli.

Measurement of Meadow Populations.—A project was then begun on which most of the conclusions in the following work are based. It was decided to measure periodically the last completely exerted leaf on ten plants with respect to blade length, sheath length, and blade width (measured 5 mm. above the ligule). Other data which later came to be recorded in detail included the lengths of the inter-

nodes and panicles on the flowering shoot, the number of leaves which were green, the nodes which bore roots, and the number of tillers and rhizomes. Measurements were begun in early March of 1949 and extended to the following March. During the spring measurements were made weekly, while during the summer, fall, and winter they were made bi-weekly or monthly. Dissection of plants under a binocular microscope was necessary to provide much of this data. To obtain the necessary rhizome material, blocks of sod were subjected to water under moderate pressure until the soil was washed away.

In order to gain preliminary information on variation with habitat, identical studies were made of grass in four situations: the unmowed meadow; a closely grazed pasture; a meter-square plot of meadow grass which had been burned over in mid-February; and a similar-sized plot which had been cleared of all surface vegetation with a sharp hoe while the ground was frozen in February. Although information on all of these plots is not included in the present study, an understanding of the basic trends was facilitated by these measurements and observations.

Supplementary Observations.—Data obtained from the above measurements were supplemented in several ways. Exclosures¹ were placed in pastures being grazed at various times of the year to determine the repercussions of different types of grazing management. Also, a special box was made which had glass sides that could be darkened by inserting a tight-fitting panel. This box was filled with dirt and several plants of bluegrass were placed against the glass. By removing the panel their underground activity could be watched throughout the year.

Information has also been derived from examination of grass plants growing under unique environmental conditions. Plants that grew in soil on which urine or manure had fallen, or that sent rhizomes into mole tunnels, or which had been grazed closely by mice in their winter pathways, or had been covered with alluvium, or grew in deep shade or in very dry or wet localities, have all contributed small bits of important data.

Laboratory Investigations.—In general, laboratory experiments were designed with the idea of finding out how rhizomes grow and what makes them turn up. Some data on leaf growth were also obtained in connection with this work. Bluegrass rhizomes were grown in two ways: separated from the parent plant and grown in water or various solutions in test tubes or Petri dishes; or left attached to the plant and allowed to develop in a natural manner except that they were enclosed in glass tubes so that they could be measured, protected, and identified. Some experiments were made in which these tubes were filled with nitrogen, water, or air.

To obtain as much control over bluegrass plants as possible, some were grown in bottles containing nutrient solution. These were kept under constant light and temperature conditions. In nature, the base of the bluegrass plant, together with its roots and rhizomes, is underground and thus invisible. In searching for some

¹An exclosure is a part of an experimental area which is fenced to eliminate the influence of certain animals, in this case livestock.

manner of exposing these underground parts without too greatly disrupting their natural relationships it was discovered that ordinary "Even-Flow" baby bottles had peculiar possibilities. The nutrient solution could be placed in the bottle and the plant could be held in place above by inserting it through a slightly enlarged hole in the nipple (pl. 2, fig. 1). This would allow the basal part of the plant to be within the nipple and thus protected from desiccation. At the same time, by coating the nipple with opaque paint the inside was kept quite dark, thus simulating soil conditions. The roots could extend into the nutrient solution below and the leaves into the light above.

Rhizome growth was provided for by making five perforations at the base of the nipple, just above the plastic cap, and in these inserting short pieces of $\frac{1}{8}$ -inch glass tubing which were connected at the other end to a $\frac{1}{2}$ -inch glass tube, about 7 inches long, with a 1-hole stopper in the end (pl. 2, fig. 2). As a bud on the basal part of the grass plant was seen to be developing into a rhizome it could be guided into the small glass tube and then would grow out into the larger tube where various experiments and observations could be conveniently made. A perforation was made down through the cap and nipple so that an air-supplying tube could be inserted into the bottle. Saturated air under low pressure was bubbled into the nutrient solution through a fine glass capillary. This air, in escaping, flowed around the roots and base of the plant and out through the rhizome tubes and served to keep the water aerated and the atmosphere in the tubes moist at all times. A light-tight box high enough to accommodate the bottles was then constructed and in the top surface were cut twelve holes spaced on a 9-inch grid (pl. 2, fig. 3). These holes were just large enough to receive the bottle caps. One side of the box was removable so that bottles full of nutrient solution could be inserted into the openings from underneath. The height was made just sufficient so that when the cap was screwed on the bottle, the rhizome tubes inserted into the nipple would rest on the top surface of the box (pl. 2, figs. 2-4).

New rhizomes which had been turned up long enough to form two good leaves and several roots were obtained from a single clone of bluegrass and were inserted into the nipples in such a way that their roots contacted the solution while the bud region of the plant was in the air opposite the openings for rhizomes. In order to keep light away from any rhizomes which might develop, it was necessary to construct a false top of removable panels (pl. 2, figs. 4-5). By loosening a thumb screw these panels could be removed so that access could be had to the rhizome tubes and bottle caps. A fluorescent fixture containing six 15-watt tubes was placed at a height of 30" above the plants (pl. 2, fig. 3).

This battery of bottles was kept first at a constant temperature averaging 70°, and then later at 40°. Variation was not ordinarily more than 5° in either direction. Day length was fourteen hours during most of the experiment but was reduced to twelve hours during the last three weeks of the 40° temperature.

The nutrient solution used was that given in Meyer and Anderson (1941), and was changed every two weeks. A 5 per cent iron solution, made up of equal

quantities of FeCl_3 and tartaric acid, was added weekly. No difficulty was had in getting plants to grow, though the light intensity was apparently insufficient for normal growth, and the leaves were rather lax. The low light intensity at the 70° temperature was not conducive to elongation of buds or roots, while at 40° roots grew well but budding was largely restricted to aerial shoots instead of rhizomes. There was no opportunity for further experiments under more optimum conditions for rhizome production.

LITERATURE

The importance of Kentucky bluegrass as a lawn and pasture grass in northern Europe (especially in Germany and Sweden) and in the northeastern part of the United States has led to many studies on various aspects of the plant. Most of this research has been concerned with seed and forage yields and chemical content under different treatments and seasons. A great deal of intensive genetic work (see Brittingham, 1943) and histological work (see Nielsen, 1946) has been done in connection with its apomictic method of reproduction. Considerable research on bluegrass variation (Smith et al., 1946), taxonomy (Mecenović, 1939), and germination (Gassner, 1930) has also been published.

Somewhat less information is available on the life history of the plant, its seasonal activities, and its manner of growth. Nishimura (1923), in a comparative study of the morphology and development of *Poa pratensis*, *Pbleum pratensis* (timothy), and *Setaria italica* (millet), anticipated by many years subsequent work on the species. Close observation and detailed drawings of the seedlings, the basal region of the plant and of the developing inflorescences were made. Some discussion of germination and roots and the first mention of polyembryony were also included.

Wieland (1926), in connection with an intensive study of variation, necessarily devoted some attention to the gross morphology of the grass, but was not concerned with how it got that way nor how it changed with the season. W. L. Brown (1940), also dealing with variation in the species, traced the seasonal development of two strains from March to October.

Musgrave (1940), in an unpublished thesis on the life history of bluegrass, discussed various aspects of germination, leaf, shoot, rhizome, and inflorescence development, also differences between plants grown as spaced seedlings and in undisturbed sod. Evans (1949) discussed his investigations on bluegrass over a long period of years, including various aspects of its life history and of the influence of environmental factors on its growth. He summarizes information on rhizomes, roots, inflorescences, photoperiodic relationships, and annual cycles of growth, development and reproduction.

Work on the physiological aspects of bluegrass growth has been done by Brown (1939, 1943), Harrison (1934), Peterson (1946), Peterson and Loomis (1949), Phillips (1943), Darrow (1939), Naylor (1939), and others.

Practically no information exists on the developmental anatomy of bluegrass.

The best work of this sort has been done by Sharman on maize (1942) and on *Agropyron repens* (1945 and 1947). He has given close attention to the relationship between the progress of anatomical and morphological events, has emphasized the existence of a common fundamental ground plan in grasses, and has shown how slight changes can produce plants which appear wholly different. McCall (1934) has discussed the developmental anatomy and homologies of various structures in wheat with special reference to the seedling.

Evans and Grover (1940) reviewed much of the literature on the developmental morphology of grass and discussed terminology and general concepts of growth with special reference to the inflorescence in a number of species. Bonnett (1935, '36, '37, '40) and Noguchi (1929) have described and illustrated various aspects of the development of the inflorescences of the small grains and maize. Prat (1934, '35) examined the anatomy and morphology of the grass culm and discussed certain theoretical aspects of its growth. He expressed various correlations, and discussed maturation of tissues.

Certain aspects of the developmental physiology of grass growth have been discussed by such workers as De Ropp (1946), Weintraub and Price (1947), and van de Sande-Bakhuyzen (1937). Important life histories of grass plants include those of Percival (1921) on wheat, Weatherwax (1923) on maize, and Evans (1927) on timothy.

BLUEGRASS IN SIMPLEST TERMS

The Sod.—When we look down at the leaves of grass they merge into a confusion of green (pl. 3, fig. 6). What does an individual bluegrass plant really look like? If we take up a 6-inch square piece of sod the question remains unanswered, for, even after the dirt has been washed away, there is left a confusion of roots and strong wiry underground stems that criss-cross in every direction (pl. 3, fig. 7). These stems seem to connect the various aerial leafy shoots in a haphazard manner. Occasionally they are seen to branch, and some may be white at the tip, showing that they are still pursuing their subterranean destinations. These wiry interwoven stems are called rhizomes, and they are one of the reasons why sod can be rolled up in a ball. They are also one of the reasons why studying an individual bluegrass plant is difficult.

A Single Plant.—If we start with a seedling the problem is simple, but eventually we shall have to deal with the vegetatively spread individual. For our purpose only the gross features of the seedling are significant. Pull a six-weeks-old plant from the soil. It is about as simple as bluegrass ever gets (text-fig. 1A). It has a beginning and an end; it has shed its nourishing grain and become autonomous. It will have four or five narrow spreading leaves which are bundled together toward the base for about one-half of their length. At the bottom of the bundle are roots. If we are used to plants which have stems we shall be disappointed when we pull the leaves apart, for they enclose only the bases of other leaves. At the center of the bundle, at its base, with its tip barely visible, is a

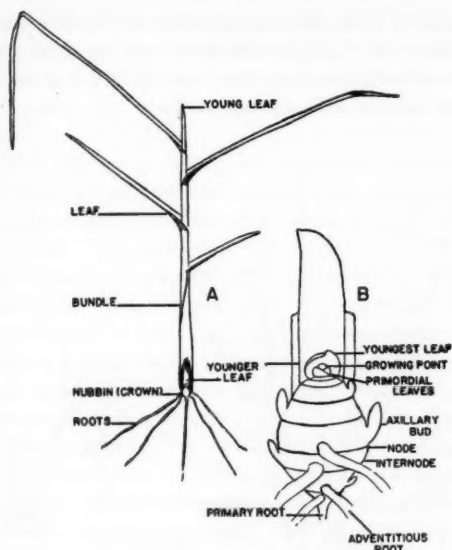


Fig. 1. A six-week-old bluegrass plant—about as simple as bluegrass ever gets: A, seedling, $\times 2$; B, crown, $\times 13$.

young, rather yellowish green leaf which is in the process of growing out into the light. Its tip is darker green but it is not yet bent outward as are the other leaves. Within this elongating leaf is a *younger* one only a few millimeters in length and inside of it is the minute *youngest* leaf which protects the nested primordia of two or three future leaves. At the center of this nest is the small bulbous *growing point* of undifferentiated cells, from which the primordia arise. These structures are shown in detail in text-fig. 1B.

The only stem the plant possesses is the *nubbin* of solid material to which the leaves, the growing point, and the roots attach. This nubbin, or *crown*, as it will be called, may be only a millimeter or two in length. Under magnification it is found to be a systematically organized structure with bilateral symmetry, holding alternate leaves and enclosing at the base of all but the lowest one an *axillary bud* (text-fig. 1B). These leaves and buds seem to arise from successive horizontal partitions on the crown which are termed the *nodes*. Separating the nodes are the *internodes*, sections of stem which, while sometimes much elongated, here are scarcely distinguishable.

From each of the lower two or three nodes a pair of roots arises, one root on each side of the axillary bud. These are the *adventitious roots* which play a major role in feeding and anchoring the plant. In all young seedlings there is also a *primary root*, the first root of the newly germinated seed, which persists for a short time at the basal tip. In many species of plants this primary seedling root develops

into a taproot by which such plants are permanently fixed to one spot. But bluegrass is not tied down for a lifetime of sitting on top of a taproot; instead, its liberated stem can develop roots wherever an axillary bud exists, and can thus gradually shift position and still maintain itself.

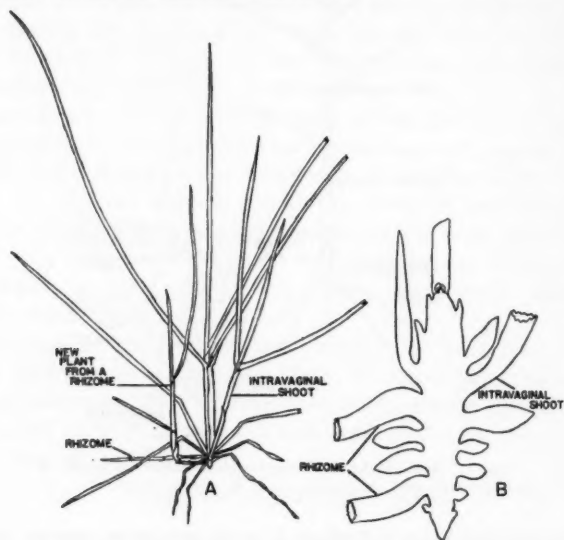


Fig. 2. A spring seedling in its first fall: A, the plant, $\times \frac{1}{2}$; B, crown, \times about 5.

The Appearance of Branches.—When we examine the spring seedling late in the fall of the same year (text-fig. 2A and B), we find that the story has begun to be a little more complicated. The apical growing point is no longer the only active one. Some of the axillary buds, of which there may be 10 or 12 by now, have begun to grow. Thus bluegrass, like most plants, produces branches. A bud has a choice of two destinies. Which it follows depends upon where it is situated. In the fall those buds which are enclosed at the base of the most recent two or three green leaves will send up vertical leafy shoots within the secrecy of the retaining leaves of the parent plant. A few of the lower, older buds borne in the axils of leaves which are dead will develop, or may already have developed, into non-leafy horizontal shoots. The upward-growing branches, or *tillers*, are sometimes called "*intravaginal*" shoots because they arise within the confines of the sheathing base of living leaves. The horizontal shoots are "*extravaginal*" and protrude through the base of the dead sheathing leaf if it is still attached. These are the *rhizomes* which, as we have seen, grow underground. Sooner or later they turn up to form new plants quite similar to the parent.

The differences between tillers and rhizomes are easily seen. One rises in the axil of a green, living leaf, one in the axil of a dead or dying leaf. The most

distinguishing feature of the rhizome is that it has short colorless scale-like leaves and has a distinct stem made up of a series of fairly long internodes, while the upright intravaginal shoot, or tiller, bears normal green leaves and has a very much condensed stem or crown, just as did the parent plant which it resembles in almost every respect.

The end result of this system of branching is that the slender static seedling becomes a mobile plant, capable both of increasing its number of leafy shoots and of extending itself over considerable area, sometimes as much as two square meters in two years time under ideal conditions. (Kannenberg and Wrede, 1934). The intravaginal shoots thicken the plant by making available more new leaf-producing places, often as many as 10, sometimes up to 50 in a season when there is very active secondary and tertiary branching. Rhizomes spread the plant horizontally, and for all practical purposes once a rhizome has turned up and developed a new leafy shoot it can be considered a new individual, even though genetically it is identical with the parent plant. It may remain attached to the parent for a considerable period, though apparently it derives practically no nourishment from it.

An interesting demonstration of this independence was provided by an experiment primarily designed for other purposes (pl. 4, fig. 8). A flower pot was filled to capacity with soil. A bluegrass plant with long, well-developed roots was placed in the pot so that the roots were covered by the soil but the crown area was left above the surface. A shallow tray with a hole in the center was placed on top of the pot, the leaves of the grass plant being arranged so that they stuck up through the hole. The tray was then filled with vermiculite, a micaceous cutting medium with practically no nutrient value. The buds on the crown were thus surrounded by mica. The soil was kept moist by setting the pot in a shallow dish of water. The mica was watered separately. After the plant became established, rhizomes began to grow out into the vermiculite and turn up along the edges of the tray. It was consistently noticed that after turning up, these new plants grew only very weakly and their leaves were very short, yellowish, and narrow. The parent plant, in the meantime, was deep green, long-leaved, and healthy. Eventually most of the offspring in the tray succumbed. There was no evidence that the vigor of the parent could be conveyed to the second vegetative generation through the rhizome, once it had turned up.

Flowers Develop.—Some time during winter, after intravaginal shoots have been initiated, metabolic changes occasioned by cool weather and short days induce "mature" growing points to begin a process of proliferation which eventually ends up in the appearance of a flowering head. This is a slow sequence of events which begins with a slight elongation of the growing point, the suppression of leaf development, and formation of many small buds which don't elongate (pl. 4, fig. 9). This is the secret winter beginning of the seed-bearing "*panicle*" which becomes so prominent a feature of bluegrass during the month of May. With the advent of longer days and warmer weather multiplication of panicle buds ceases, flower development begins at the end of each bud, and elongation of the panicle

branches takes place. When this is finished, the whole panicle is thrust out of its retaining leaves atop a flowering stalk (pl. 4, fig. 10). This stalk is called a "culm" and is part of the main axis which has become greatly elongated. Finally the plant has achieved a conspicuous stem, but only at the price of its own future, since the panicle terminates the growth of the crown's growing point. A plant in its second spring will thus be slightly more complicated than its fall progenitor, because, besides having attached to it various satellite plants in the form of tillers and rhizomes, it will be developing a flowering shoot. The mature individual can thus be said to show three types of shoots: the fall rhizome, the tiller, and a central culm, topped with a panicle (text-fig. 3). All these derive from the basal nubbin of telescoped internodes, the crown. After the inflorescence dies down, the rhizomes and tillers assume the role of perpetuating the plant. Each of these pursues an essentially independent course from then on, and eventually are separated by the decay of the parent.

THE STRUCTURAL UNITS

Leaves.—The leaves of the bluegrass plant have been described as narrow and spreading, but bundled together toward the base. It is useful to distinguish the green spreading parts as the *blades* (or *laminae*) from the lower colorless *sheaths* which in clasping each other form the bundle. The sheaths are slightly compressed tubes, while the blades are flat or folded straps. Successive sheaths enclose each other, but the blades bend outward at their junction with the sheath (pl. 5, fig. 11). A characteristic structure called the *ligule*, a membranous, valve-like flap of tissue, is found at this union and looks like a brief continuation of the sheath beyond the base of the blade (pl. 5, fig. 12).

There are no obvious anatomical differences between sheath and leaf, although, according to Sharman (1942), there is some consolidation of the many small (basipetal) strands of the blade at the ligule and consequently fewer strands in the sheath. In general, however, he minimizes the differences between the two parts. Prat (1935), on the other hand, states that the epidermis of the sheath is more differentiated than that of the blade, and that there is a striking similarity between the epidermis of the sheath and of the internode. In any case, it is apparent that the blade is the primary photosynthetic organ and is always green, while usually the sheath is green only in the vicinity of the veins, if at all.

Just how such a structure as a leaf arises and becomes differentiated into sheath and blade has been well told in detail by Sharman (1945). Although his work was done on *Agropyron repens*, his description of leaf development agrees with that of bluegrass given by Musgrave (1940). Mention has been made of the nest of leaf primordia and the central growing point which lie hidden and protected within enclosing leaves at the apex of the bluegrass crown. The activities of this critical region must necessarily be understood if we are to interpret correctly the growth of the plant as a whole.

The bulbous, translucent growing point (pl. 5, fig. 13) is the source of life,

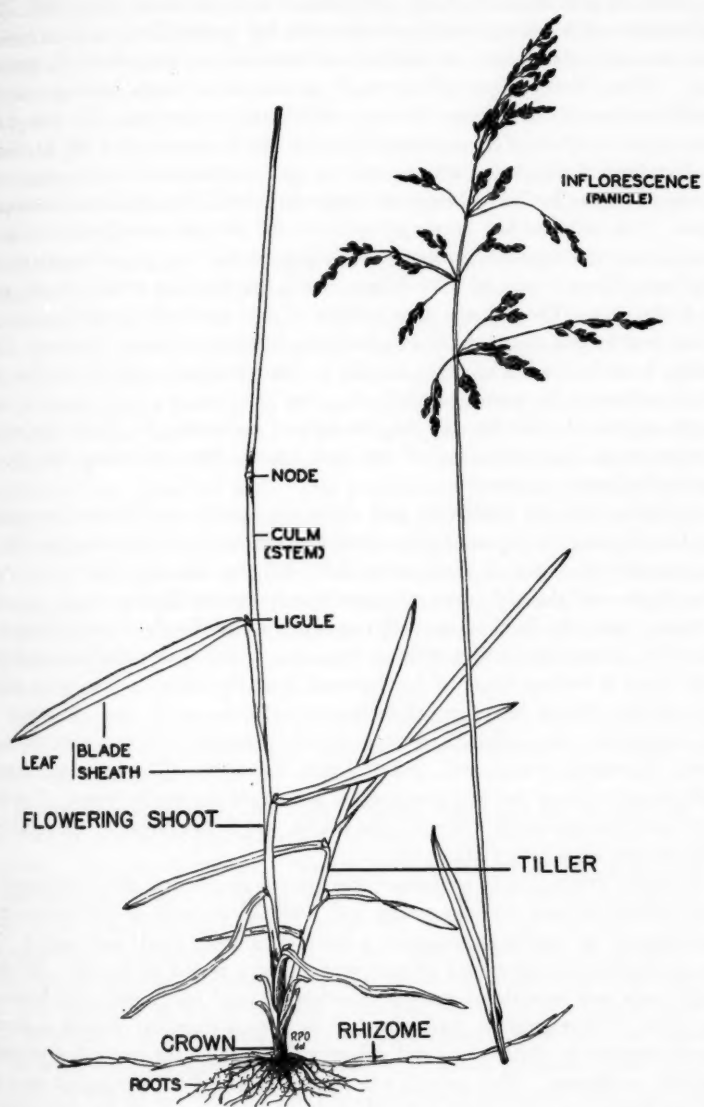


Fig. 3. A mature bluegrass plant showing the three types of shoots which develop from the crown.

the source of new undifferentiated cells from which the plant is fashioned. The first evidence of differentiation occurs when the leaf primordium begins to develop. This starts out as a number of localized cell divisions on one side of the growing point. These divisions produce a small protuberance which soon spreads out laterally, eventually becoming a crescent and finally a complete collar around the growing point. Two of these primordial leaves can be seen in pl. 5, fig. 13. Since the first formed midsection of the collar is able to maintain its advantage over the wings, the collar has an eccentric appearance with the midsection somewhat higher. This incipient leaf grows primarily by cell division at its base and to some extent by a short-lived meristematic band along its tip. As growth continues the collar soon forms a sort of loose-fitting, parka-like hood or cowl over the apex (pl. 5, fig. 14). Through the face opening of this parka the growing point can be seen, and by this time it will have given rise to one or two new crescents. This opening is at first quite minute, .2 mm. or less, just large enough to allow the collar to slip over the growing point. At about this time the leaf is supplied with its primary vascular bundle, and the thin fold of epidermis, the ligule, first makes its appearance at the junction of leaf and crown, thus indicating that sheath tissue is beginning to develop.

Growth of the leaf blade (the part above the ligule) soon becomes very rapid. The face opening of the hood is so stretched out as the blade elongates that it becomes unrecognizable in the mature leaf. Between the time that active elongation begins and the leaf grows to maturity only two or three new leaf primordia develop.² Since the hood stage itself represents about the third primordium in a series it is evident that under ordinary vegetative conditions there are about five or six leaves in various stages of development from the newest collar to the newly matured leaf. These leaves would measure roughly about .1 mm. (crescent), .2 mm. (collar), 1 mm. (hood), 4 mm. (blade beginning to elongate), 50 mm. (sheath beginning to elongate), and 120 mm. (mature). The last two measurements are given only for easy comparison and might be much longer. The first three leaves are waiting in line while the fourth and fifth elongate. The blade and sheath of the sixth have fully matured.

De Ropp (1946), in an analysis of the growth of the first blade and sheath of a rye seedling divided the very young leaf, while it was still in the embryo, into equal sections by marking them with a mixture of lamp black and vaseline. He then made daily measurements of each section for a period of a week. His data showed very well how sheath-growth was delayed until leaf-growth had begun to slow down. It was apparent, however, that the change from leaf-growth to sheath-growth was not an abrupt one, and the growth curve of the entire leaf remained relatively unaffected. This growth was primarily one of cell elongation, since no new cell division was noted after the third day. De Ropp concludes that ultimate leaf length depends on the activity of the basal meristem during the first three

²The interval between the appearance of successive leaf primordia is commonly termed a "plastochrone."

days. This period of cell division undoubtedly varies greatly with species, environment, and season. De Ropp has also called attention to the difference between the manner of elongation of the blade and the sheath. In the sheath it was found that each marked segment contributed about equally to the mature organ. In the blade, however, the basal fourth of the marked primordium contributed three-fourths of the total growth, while the tip segment scarcely enlarged. This may in part demonstrate why the tip of grass leaves is frequently slightly boat-shaped. Apparently, the primordial hood elongates so slightly that its original structure is more or less preserved.

A mature vegetative leaf is thus the product of two growth processes, the elongation of blades and elongation of sheaths. The two processes do not happen to the same leaf at the same time. What actually happens is that an elongating blade (leaf No. 4, for example,) and the sheath of the enclosing older leaf (leaf No. 5) elongate simultaneously and at the same rate so that there is no necessity for the tender young blade point to push up alone through the close confines of the sheath bundle. Instead, the two grow up together. Upon dissection of leafy shoots, the tips of young leaves will generally be found to be just about even with the ligule of the preceding leaf. This is additional testimony to the essentially similar growth rate of blade and sheath. But the sheath does not grow as long as the enclosed blade, and consequently as the sheath matures and its growth stops, the blade within continues its growth alone out into the light. It often happens that the tender new blade is not strong enough to start pushing out of the orifice of the ligule, and the tip of the leaf becomes cramped and crinkled into one or more small folds. These folds remain impressed in the leaf after exertion and are commonly seen on rank-growing bluegrass.

Under vegetative conditions no blade-sheath pair begins to elongate until the previous blade has stopped growing. This has some significant repercussions which will be discussed in detail later.

Phytomers.—Bluegrass is not built of leaves alone. A leaf is only the most obvious part of a more fundamental structural unit called a *phytomer*,³ or plant segment. This unit consists of a piece of stem with a leaf on the upper end and a potential bud or shoot at the lower end. If the leaf is on the left side of the stem at the top, then the bud will be on the right side at the base. There are complementary sections with the leaf on the right and the bud on the left. The two types of sections alternate with each other and produce the characteristic bilateral symmetry of the grass plant (text-fig. 4A and B). Another result of this alternation is that the bud of the segment above rests within the concavity of the leaf below, just above the point where the leaf is attached. This concavity is called the *axil* of the leaf and the bud is therefore commonly called an axillary bud. Though this name is a convenient one, it encourages the idea that a leaf

³*Phy'to mer*, a term according to Evans and Grover (1940) used as early as 1879 by Asa Gray to designate a structure which, when produced in a series, makes a plant of a higher grade. The term was also employed and described by Weatherwax (1923).

and its axillary bud are closely related, when actually from an anatomical and physiological standpoint the association between a bud and the leaf above, on the opposite side, is much closer. Sharman (1942) has provided anatomical evidence supporting this.

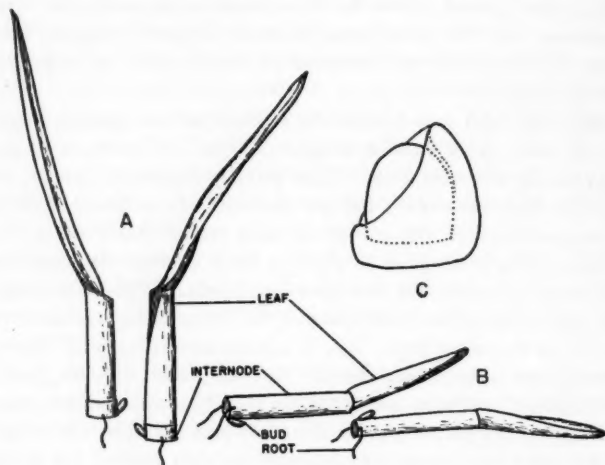


Fig. 4. A and B, complementary phytomers or grass-building units, A, from a vegetative crown, B, from a rhizome; C, the hood leaf which protects the growing point.

Where two phytomers join together a node is formed. The phytomer axis thus becomes an internode which may be long or almost undiscernible. Each phytomer, in addition to its leaf, internode, and bud, is theoretically capable of producing roots at its lower end, usually one on each side of the bud.

Phytomers have their beginning at the growing point. A leaf primordium is the first visible evidence that a new phytomer is forming. The small hood leaf which has been described is not just a shell of tissue tacked on the apex but actually can be visualized as a sort of kettle-shaped structure with a bottom made up of undifferentiated cells produced by the growing point. Inside this kettle new phytomers continue to begin their differentiation as cells in the meristematic point (text-fig. 4C). The course of differentiation and maturation in a phytomer, as Sharman (1942) has shown, is a diagonal one which begins with the development of the leaf at one side at the top, then proceeds to the internode, and passes on to the bud on the opposite side at the base. When roots are present they are the last organs to be formed (text-fig. 5). This course of phytomer development has its basis in the maturation of various anatomical units, especially the vascular system. By the time one phytomer has matured, several others will have begun their dif-

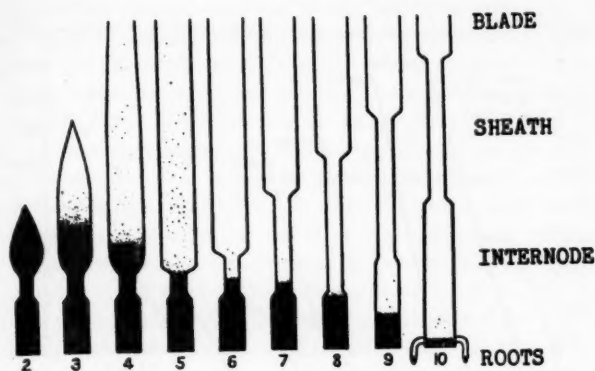


Fig. 5. Diagram illustrating the wave of elongation and maturation passing down the blade, sheath, and associated internode in *Zea Mays*. Solid black indicates the more actively dividing tissues. (From Sharman, 1942).

ferentiation. The exact number depends on the stage of maturity of the plant. Plants ready for flower initiation may have as many as eight or nine segments in various stages of elaboration, while, as we have seen, a vegetative plant may have only five or six readily discernible.

The diagonal course of development is outwardly apparent when we measure the elongation of the different phytomer elements, as van de Sande-Bakhuyzen (1937) has done for wheat. It has been said that the blade elongates first, and is followed by its sheath. In text-fig. 6 the whole leaf has been measured as a unit; consequently successive leaves overlap (or *would* overlap if the growth curve were extended to its origin). This overlap represents that period of time when a sheath and the new blade which it encloses are growing up together. Where there is no overlap, the leaf has grown out of the sheath and continued its growth alone.

The internode may or may not elongate, depending on where it is located on the plant. If it does elongate, it does so only after the leaf has matured. Under vegetative conditions, as in the rhizome, and in the early reproductive phase as shown in text-fig. 6, only one internode grows at once. Under the influence of the inflorescence, however, there is a tendency for some overlap of elongation in those internodes just below the flower head. In bluegrass the last three internodes elongate more or less simultaneously. An overlap has also been recorded by Sharman for maize (1942) and *Agropyron* (1947), by Prat for rye (1935), and is suggested in the last two nodes of wheat (text-fig. 6).

A grass plant thus develops by virtue of its ability to produce new phytomers and to elaborate the plastic organs situated thereon. The remarkable plasticity and independence of these units make possible the varied appearance of different grasses and the different parts of the same grass. This will become apparent with the following description of the three main shoot types in bluegrass.

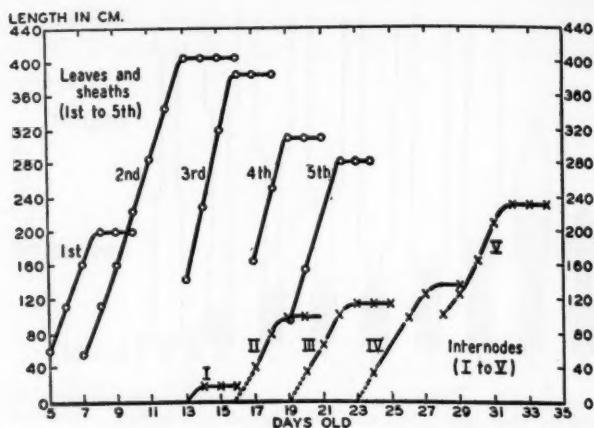


Fig. 6. Growth in length of leaves and internodes of wheat. (From H. L. van de Sande-Bakhuyzen, "Studies on Wheat Grown Under Constant Conditions," Food Res. Inst. Misc. Pub. No. 8, p. 102. Stanford University, Calif., March 1937).

THE RHIZOME

What Does It Look Like?—A rhizome is by definition an underground stem. In bluegrass this means from a few millimeters to several centimeters underground. It may grow horizontally below the surface for 6–12 inches; it may merely swing out and up in a short inverted arch; or occasionally it may turn up abruptly without making any lateral growth, in which case it should probably be considered merely an extra-vaginal shoot. Plate 6, fig. 15, shows rhizomes of these three types on a single plant. The fact that the rhizome is a stem imposes upon it certain responsibilities. It cannot pursue its underground path by simply adding cells at its tip as does a root. Its growing point is obliged to produce phytomers, which in turn produce leaves, internodes, nodes, buds, and roots. The rhizome thus becomes a jointed structure with various appendages rising from the vicinity of its nodes. Internally the separate phytomers are bound together by a complicated vascular system.

The most prominent parts of the rhizome are the elongate white internodes, which, in series, make up the axis. These average 1 or 2 cm. in length, are solid, and are frequently rather flattened in cross-section. The tip of this underground stem is like a sharp white awl and is well suited for penetrating soil (pl. 6, fig. 16). This tip is actually a much-reduced leaf which has no blade. It is essentially a closed tube although a minute pore is present at the tip. It serves well as a sort of caisson within which the subterranean growing point can work to lay down building material and elaborate new structures. When a new rhizome leaf has been fashioned inside, it penetrates the caisson, which then splits and dries up. On

the older parts of the rhizome these leaves hang loosely at each node and become weak brown remnants scarcely recognizable as foliar structures. They are given the special name of *cataphylls*, or scale leaves. These cataphylls are arranged on opposite sides at successive nodes, and partially conceal the internode of the next phytomer (text-fig. 7). In the axil of most cataphylls is an axillary bud, though occasionally no such structure can be found, especially at the first few nodes. A pair of roots usually appears at each node, one root on either side of the bud.

The first two or three internodes nearest to the parent plant are quite short, less than 1 or 2 mm. The next few are intermediate in length, while subsequent ones may range from 1 to 30 mm., apparently depending largely on the amount of water available to the plant. The sequence of cataphyll lengths is essentially similar to that of internodes. At the junction of the main shoot and the rhizome is found the first scale leaf, if such it may be called (text-fig. 8). It has only two prominent veins and arises from the upper side of the rhizome with its back to the crown. It is minute, less than 1 mm. in length, and slightly heart-shaped when it has been broken open. Presumably, it is the undeveloped *prophyll* which will be more completely discussed with reference to intravaginal shoots. The next scale leaf is a short structure, about 2 mm. in length, and is the first true cataphyll. It is well supplied with vascular strands as any legitimate leaf should be. This cataphyll and its axillary bud are not located on the opposite side of the rhizome from the prophyll but are turned only one-fourth of the way around so they are on the side instead of underneath (text-fig. 9). Succeeding cataphylls then alternate first on one side of the rhizome axis and then on the other. If this quarter-twist were not put into effect the axillary buds on the rhizome would point up in the air or straight down in the soil. The first few cataphylls are rather short, but later ones average just slightly longer than their internodes. Cataphylls do not vary nearly so much in length as do the internodes, nor do they appear to be so sensitive to water shortages.

How Does the Rhizome Grow?—The scale leaves are produced from the growing point of the rhizome in the same manner as described for ordinary leaves, except that blades do not develop. When a crown bud has been stimulated to grow into a rhizome, the small enclosing prophyll is broken and successive cataphylls elongate, though only one at a time. Each new scale leaf is a whitish cylinder which tapers to a strongly pointed tip. Since the new cataphyll develops within the previous one (text-fig. 10) there comes a time when penetration must occur. Consequently, the retaining point of the rhizome is broken open at the tip permitting the next cataphyll to appear.

Two main processes occur on every phytomer: one is leaf growth, one is internode growth. On the rhizome, elongation takes place first in the cataphyll, then in the stem behind it, thus following the pattern described for phytomers in general. The scale leaf is extended not only by its own growth but by that of the internode below. It can be seen, therefore, that the penetration of one cataphyll by another is not simply a matter of one leaf growing up inside the other but is the product of two separate forces, leaf elongation and stem elongation.

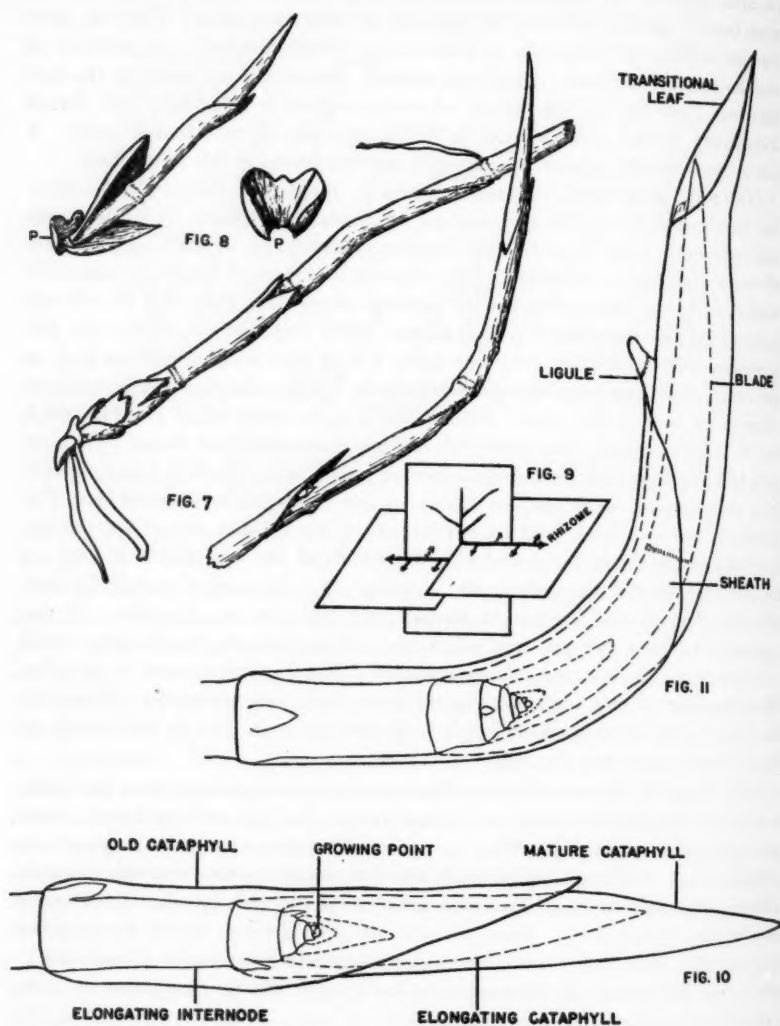


Fig. 7. A rhizome, $\times 4\frac{1}{2}$. Fig. 8. First leaves of the rhizome, $\times 4\frac{1}{2}$ (P, prophyll). Fig. 9. Showing the arrangement of branches and buds on the bluegrass plant. Fig. 10. Diagram of a rhizome tip. Fig. 11. Diagram of a rhizome tip which has begun to produce cataphylls tipped with blades and is turning up.

One might describe the growth of the cataphyll as the forging of a steel tip. Once the tip is forged the developing internode serves as a shaft by which the tip is pushed out of the old cataphyll and through the soil. While this is going on, a new point is again being forged within the confines of the tip in use. Sooner or later the tips of the cataphylls become more delicate, a little less conical and a little more flattened. Upon close examination it will be seen that the point (only 1 or 2 mm. in length) is no longer a complete cone with a small pore, but is slit down one side (pl. 6, fig. 17). Furthermore, if we open this slit carefully we will find the slit point is separated from the rest of the cataphyll by a thin perforated membranous diaphragm which is the ligule. This new, longer, open point thus represents the first beginning of a leaf blade on the cataphyll. It is common to find many cataphyll leaves tipped with very short blades, but wherever this tip, by virtue of the removal of some physiological block, is allowed to reach a length of 4 or 5 mm. it is apt to be associated with a curving up of the rhizome and with its prompt appearance at the soil surface (pl. 6, fig. 18).

How Does It Turn Up?—In many respects we should not speak of a rhizome's turning up at all, for very little, if any, bending originates in the internodes, nodes, or cataphylls of that structure, even though they may become secondarily curved by playing follow-the-leader with the new blade (text-fig. 11). This blade, in contrast to the indifferent sheath, has a strong objection to gravity, and as soon as it has exceeded the limitations of its enclosing cataphyll it shows this prejudice by striving to reach upward to the soil surface. This change from no blade to a fairly long blade (several cm.) is sometimes a sudden one, in which event only one leaf is required to make the break. The fact that the longer blade is usually associated with a longer sheath makes this a possibility. On the other hand, progress toward a long blade is sometimes slow, and two or three leaves may be involved in the effort to reach above ground.

Once a bladed leaf reaches the light, no elongation of the internode beneath ordinarily takes place. Light, working through the blade, prevents internode growth. Weintraub and Price (1947) investigated the physiological basis of such inhibition in the oat seedling and showed which wave lengths of light cause the inhibition, but they did not isolate the photo-receptive substance. If blade-tipped cataphylls do not reach light, the associated internode will elongate. When a leaf with a long well-developed blade is prevented from reaching the light by being covered with soil, manure, or other debris the internode will become abnormally long (text-fig. 34). Where the transition from cataphyll to aerial leaf is abrupt, the rhizome shoot has a characteristic abrupt right-angled appearance, but where the transition is slow and internode growth takes place within the upbending leaf, the rhizome is gracefully curved. The manner of turning up, which varies greatly with habitat and strain, has a distinct influence on the depth and angle at which the crown of the subsequent shoot comes to rest.

Every aerial leaf which develops from the underground growing point follows the course of the transitional leaves, since each new leaf blade arises within the

previous sheath. Successive leaves increase in length, and later development of the crown is similar to that already described for the seedling. In pl. 6, fig. 18, the last roots on the top rhizome indicate the position of the growing point within enclosing sheaths.

The most important result of this turning-up process is that the growing point of the shoot is usually left submerged in the soil to a depth of 1-3 cm. This is of great value to a pasture and lawn plant which must withstand close grazing, treading, and mowing. Of significance also is the accumulation of a well-protected reservoir of subterranean buds in the crown area which can provide new rhizomes on a minute's notice. It will be noted in text-fig. 11 that usually the rhizome axis remains essentially horizontal and its buds point in the same direction as the rhizome. This exerts a directional influence on new rhizomes which develop. It explains in part the maintenance of a general similarity of direction from one generation of underground shoots to the next. As the shoot becomes older the crown becomes more vertical and the buds more crowded; new shoots then develop in almost any direction.

Why Does the Rhizome Turn Up?—The turning-up of a rhizome is usually not due to the influence of the environment on the rhizome itself, although mechanical obstruction sometimes plays a small part. Instead, turning-up seems to be correlated with some physiological development within the parent plant. Sharman (1947) has mentioned the fact that light reaching the rhizome was not the deciding factor in *Agropyron repens*, for rhizomes of that species will continue to grow horizontally (though they turn green) when the soil around them is removed. Similarly, above-ground stolons of many grasses and rhizomes of other plants such as the common *Sansevieria* have reduced leaves and remain prostrate regardless of their being exposed to light.

With bluegrass, rhizomes artificially exposed usually begin to form blades and shorter internodes, and soon turn up. The number of transitional leaves, however, may vary considerably. That the rhizomatous habit in this species apparently hangs in a fairly delicate balance is suggested by various experimental results and observations. Harrison (1934) has found that rhizomes tend to be much shorter when grown in a high nitrogen medium. Brown (1939) has presented data that show decreasing rhizome length above a temperature of 70° F. and below 60° F. Heavy clipping and grazing also reduce rhizome length. In early spring and early fall, when above-ground growth becomes more proteinaceous and darker green and when carbohydrate reserves are drawn on heavily, practically all rhizomes below the ground begin to appear at the surface.

Laboratory Experiments.—In a series of experiments, the growth of rhizomes was studied under controlled conditions. The rhizomes were separated from the parent plant and placed upright in test-tubes containing a little water, or in Petri dishes on blotter paper. These were then grown in the dark, and were subjected to the following treatments with the results indicated:

TABLE I. GROWTH OF RHIZOMES SEPARATED FROM PARENT PLANT

Number of rhizomes	Aver. initial length (cm.)	Grown in	Temp. (°C.)	Days	Treatment	% increase in length
4	3	Tubes	70	14	Tube filled with water	0
4	3	Tubes	70	14	Tube filled with nitrogen	0
4	3	Tubes	70	14	Tube filled with air	50
5	6.4	P. dish	40	14	Distilled water	24
5	6.0	P. dish	40	14	Auxin, 1 mg./liter	20
5	6.1	P. dish	40	14	Auxin, 10 mg./liter	32
5	5.6	P. dish	40	14	Auxin, 50 mg./liter	28
5	5.4	P. dish	40	14	Distilled water	33
5	5.7	P. dish	40	14	Iodoacetate, .00001 m.	19
5	6.4	P. dish	40	14	Iodoacetate, .0001 m.	10
5	6.0	P. dish	40	14	Iodoacetate, .0005 m.	15
5	6.2	P. dish	40	14	Iodoacetate, .001 m.	19
9	5.0	P. dish	40	38	Distilled water	34
18	5.0	P. dish	40	38	Glucose, 1%	88

While in general the numbers of rhizomes used were insufficient to lend significance to the small differences indicated above, the response to glucose is clear, and a slight inhibiting effect of iodoacetate is strongly suggested. All rhizomes which made any growth showed a distinct tendency to turn up. Glucose rhizomes continued alive for 3½ months and eventually increased on an average of 125 per cent in length, while the distilled water controls showed almost no growth after two weeks, and were obviously dead after one month. Figure 19 of pl. 6 shows control and glucose rhizomes removed from the Petri dish for comparison.

Another group of experiments utilized the rhizome while it remained attached to the parent plant. In this group test-tubes were supplied with rubber stoppers in which there were three holes. Into two of these holes right-angled glass vent tubes were inserted. The rhizome of a bluegrass plant was inserted into the test-tube through the third smaller hole and was then sealed in with a little cotton saturated with lanoline paste. The entire plant could thus be conveniently held in place by fixing it between the vent tubes. The test-tubes with their respective plants were then placed in a flat and covered with vermiculite so that no light could reach the rhizomes. The plants were in a perfectly normal position and could produce leaves and roots in their usual manner. The bent glass tubes enabled the rhizome chamber to be filled with air, nitrogen, or water. Three tubes were left with free access to air; three were filled with distilled water and corked up; and three were flushed with gaseous nitrogen for ten minutes each week and were then sealed.

All rhizomes grew well, though all showed development of leaf blades and a concomitant effort to turn up. In some cases later leaf blades became much shorter and practically scale-like after the parents became well established. Growth averages of the rhizomes in each treatment over a period of four weeks were as follows:

Tube filled with	Total growth
Air	7 cm.
Nitrogen	6.5 cm.
Water	6 cm.

Two of the air rhizomes continued to grow for six weeks longer, increasing in length by 23 and 29 cm. There were approximately 15 phytomers on each of these, produced over a total period of ten weeks. This average of one new phytomer every four to five days is somewhat less than that achieved under completely natural conditions. In this experiment the vermiculite medium was sterile and not favorable for perfect development.

These experiments were not designed with any idea of statistical demonstration of facts, but were rather trial runs to perfect techniques. The indications are fairly clear, however, that while *isolated* rhizomes apparently will not grow in water or nitrogen they will grow to some extent in air, and will remain alive longer and grow more when supplied with sterile glucose than with distilled water only. In every case where growth occurred rhizomes began to turn up. No treatment prevented this.

Rhizomes remaining on the parent plant were able to grow equally well in gaseous nitrogen, distilled water, or air, and it happened that those in air outlived those in other media. In these rhizomes there was a strong tendency at first for leaves to develop, and for the tips to turn up. Later leaves, however, were much reduced. It is apparent that the rhizome has distinct possibilities in the field of experimental growth study, especially because of its natural independence of light. With the use of a complete nutrient solution and various hormones and inhibitors information might well be obtained on controlling factors in leaf differentiation and geotropic responses.

Internode Lengths.—The internodes of rhizomes are delicate recording devices. Their lengths are highly variable and apparently indicative of some fairly fundamental condition in the parent plant. A considerable number of rhizomes were dug up occasionally during several summers and each one was plotted on a graph on the basis of its sequence. In a given year a remarkable similarity of pattern was found to prevail in rhizomes from different plants and habitats.

Text-fig. 12 shows diagrams of a few of these underground shoots dug from several localities during July, 1948. Not only is there a similarity of pattern, but also a strong correlation of phytomer numbers. The consistent reduction in internode length to a few mm. in all of these shoots was evidently indicative of a period of drought which occurred during May and early June. In rhizomes dug up in July, 1949, no such depression of length was seen, and the possibility that day length played a part was thus eliminated. The rainfall records given in text-fig. 12 show that there was no shortage of moisture in 1949.

The conclusion that dry soil results in short internodes agrees with the observation that excessively drained sites showed shorter average internode lengths (text-fig. 13). The data of Phillippe (1943) are significant here in that they show no

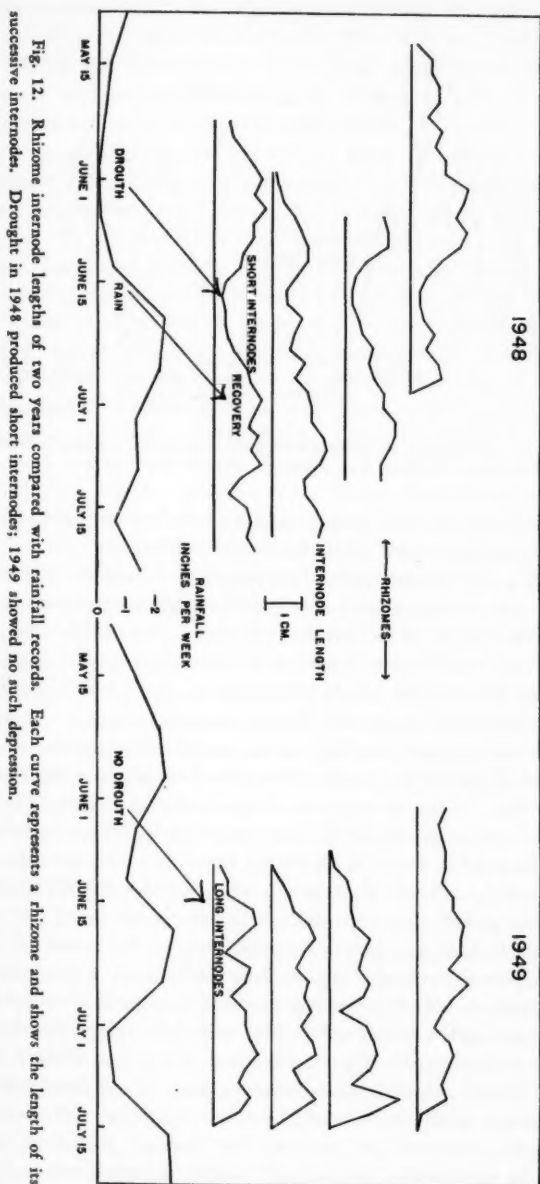


Fig. 12. Rhizome internode lengths of two years compared with rainfall records. Each curve represents a rhizome and shows the length of its successive internodes. Drought in 1948 produced short internodes; 1949 showed no such depression.

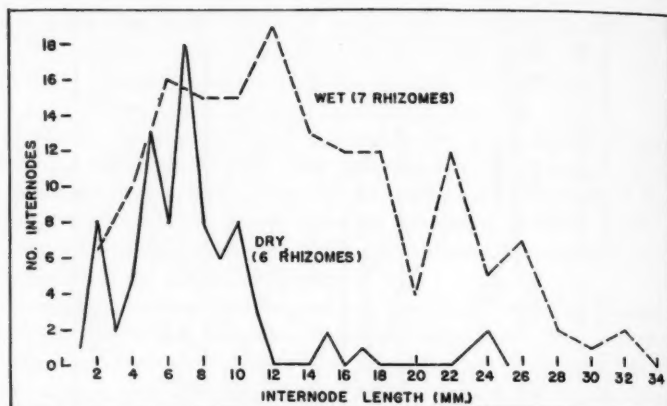


Fig. 13. The number of internodes of given lengths on rhizomes collected from two good soils, one of which was excessively drained.

correlation between internode lengths and various levels of potassium, nitrogen, or phosphorous in his nutrient solution cultures of bluegrass.

By matching and superimposing the patterns of a series of rhizomes dug up at different intervals during a year, a complete sequence of rhizome growth from some time in late May up to fall could be prepared. The sensitivity and uniformity of rhizome growth would seem to offer some interesting possibilities in interpreting the past history of a sod and related environmental and climatic conditions.

When Do Rhizomes Grow?—A seasonal interpretation of rhizome growth is not simple. About the only time that one cannot find a few rhizomes still pursuing their underground path is in late winter and early spring, and there are even some exceptions to this. Wherever rich soil is kept warm and moist during winter by circumstances such as proximity to heat pipes and buildings, or in alluvial soils close to the water table, rhizomes which are especially thick and white can usually be found. Even these, however, ordinarily turn up with the advent of spring.

There is one period when rhizomes are almost always found just beginning to grow, and that is when inflorescence elongation begins. From that time on through the rest of the summer rhizomes appear from subterranean axillary buds and grow at length through the soil. By late August most of these have turned up. At this time there is frequently a very brief flush of new short sprout-like rhizomes which are described in detail in the following section. For a few weeks in late September or early October, when the leafy tops are growing rapidly, there will usually be a second period when few new rhizomes can be found still underground. A great deal depends on just how rapid the fall flush of growth is. In dry years greening may be so slow that cessation of rhizome growth is not very abrupt, and possibly may not occur at all.

Production of rhizomes in *late* fall depends again on seasonal conditions and habitat. It is highly variable, but in general some buds do develop and grow a few inches. These late rhizomes are often caught underground, or just at the surface when the soil freezes. They then wait for spring thaws, as do the underground parts of many early-developing spring plants.

Rhizome Types.—Rhizomes are not all the same. Some turn up almost immediately without ever making a long internode and look much more like intravaginal shoots except that they do not develop inside a living leaf of the parent plant (pl. 6, fig. 15). Under a few conditions rhizomes are inclined to be *stoloniferous*; that is, instead of growing underground they grow along the surface of the soil and usually bear well-developed leaves instead of cataphylls. Those rhizomes which grow underground are also of various types. Some, such as those grown in the box, grow down and then up in a broad curve, while others grow horizontally just below the soil surface. Some are delicate and wiry, others fat, white, and flattened on the side.

Rhizomes differ greatly in their tendency to branch. Generally, in established sods axillary buds are suppressed. If the terminal bud is injured, however, then one or more of these rhizome buds develop. Under especially favorable growing conditions vigorous rhizomes will branch voluntarily (pl. 7, figs. 20 and 21, left). Evans and Ely (1935) found that in spaced plants grown in a nursery plot about 10 per cent of the rhizomes showed some branching, and that as a result of branching some clones or plants of bluegrass gave rise to as many as six vegetative generations a year. Branching also occurs when an actively growing rhizome is exposed to bright sunlight accidentally, before it is prepared to turn up. In this case branching is limited to the last few nodes, and the branches do not have long white internodes but turn green and bend upward immediately. The development of branches apparently depends on some critical balance which can be altered by environmental conditions. As with every other characteristic of the bluegrass plant variation with strain is also evident.

There are also some fairly striking seasonal differences in rhizomes. In general, summer rhizomes pursue a deliberate underground course, extending the plant to some distance. These might well be called *extensor* rhizomes. They result when a developing bud feels some distinct obligation to remain underground and not to produce leaf blades except as a last resort. Figure 21 of pl. 7 shows examples of this type. Other rhizomes might well be termed *sprout* rhizomes, for they seem to be a response to a different combination of conditions in the parent plant. They represent a sort of desperate effort to perpetuate the parent plant in the face of some adverse condition. Such rhizomes are short and are characteristically found on plants which have been injured in some manner. They may arise from a crown or from another rhizome. Plate 6, fig. 19, shows the extreme type of sprout, developed from a separate rhizome very short on food reserves. Harrison (1934) shows similar sprouts from rhizomes of plants which were injured by high temperatures. During a brief interval from late August to early September, just be-

fore rapid fall growth begins, many short sprout rhizomes appear from the crowns of plants which have been burned, grazed, or mowed too close, or, weakened by rank growth, allowed to accumulate on the sod. Such sprout rhizomes play a very essential part in the perpetuation of rank meadow bluegrass, and are especially common on those plants which have bloomed during the previous spring (pl. 7, fig. 22).

While rhizomes may be given names they themselves are not cognizant of any classification and may be intermediate in length, function, and appearance. Thus a pasture which has been grazed throughout the summer seldom contains any long extensor rhizomes. They are usually a sort of half-breed type, and are produced all summer long and well into fall.

THE TILLER

The tiller resembles a seedling or a turned-up rhizome in having green leaves and a nubbin of short root-bearing internodes at the base (pl. 7, fig. 23). This shoot arises, however, directly from an axillary bud (text-fig. 2; pl. 7, fig. 24) and not from a seed or from the tip of a subterranean stem. As pointed out earlier it develops in the axil of a living leaf.

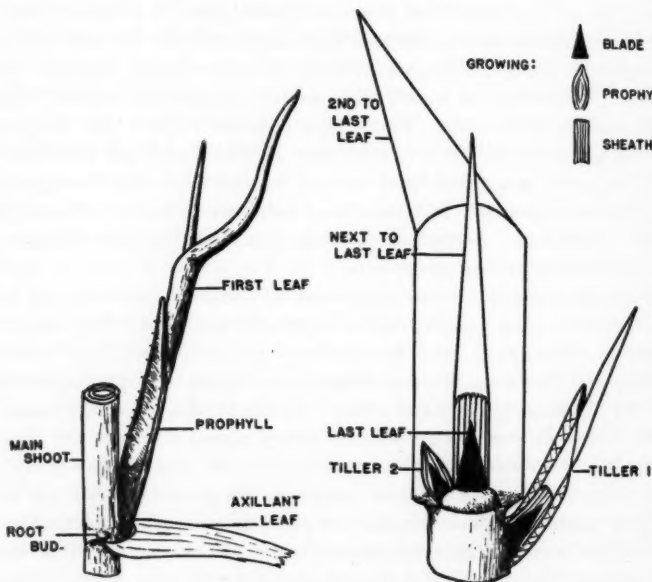


Fig. 14. The first organized structure to develop from an axillary bud is the prophyll. It sheathes the first leaf.

Fig. 15. The parts of the plant which grow at the same time during the fall "shooting season." See Table II.

The Prophyll.—Morphologically the tiller is distinctive only in the possession of a well-developed *prophyll*, or pre-leaf (text-fig. 14; pl. 7, fig. 25). This small insignificant structure is seldom seen or examined closely, for its life is short and its purpose quickly served. It is the first organized structure which develops from an axillary bud (Sharman, 1945). It does not look like an ordinary leaf for it has no blade. It is a semi-membranous sleeve, about 2 to 3 cm. long, which is flat or somewhat grooved down the side nearest the main shoot. In cross-section it is semi-circular or somewhat crescent-shaped, and at each edge of the crescent is a prominent vascular strand which extends from the base of the prophyll to its tip. Very small strands may be visible along the outer rounded edge. The prophyll is a completely closed tube except for a small pore at its tip which represents the opening left when the primordial prophyll slipped over the growing point. In this and many other respects it is similar to the cataphyll of the rhizome.

The prophyll, although the first structure to appear on the axillary growing point, does not elongate up through the confining base of its axillant leaf alone, but instead waits for the first true leaf which grows up within it. Measurements of a typical plant in process of elongating its shoots will show this synchronization.

TABLE II. PARTS OF A PLANT WHICH GROW AT THE SAME TIME

Position of leaf and sheath	Length in cm. of blade, sheath					
	Parent plant		Tiller sheath 1		Tiller sheath 2	
	Blade	Sheath	Blade	Sheath	Blade	Sheath
Last leaf	1.2*	0	.5*	0	.4*	0
Next to last	4.7	.9*	2.0	.5*	(prophyll .4*)	
2nd to last	2.7	6.0	(prophyll 2.5)			

*Indicates organs in process of elongating.

Here we see a repetition of a pattern of growth already discussed: that is, the simultaneous growth of a blade and its enclosing sheath. Although the prophyll does not exactly look like a sheath it seems to behave like one in most respects. It also bears a striking resemblance to the *coleoptile* or pre-leaf of a grass seedling (pl. 7, fig. 26) which accompanies the first true leaf of the germinating plant up through the soil and into the light. Both structures have two prominent veins and a pore at the top, are membranous, cylindrical, and have no blade. McCall (1934) has discussed this similarity in detail and has supplied anatomical evidence in support of the idea that the two organs are homologous.

Since no studies of the course of prophyll growth have been made and in view of the evidence that coleoptile and prophyll are basically similar, a growth curve (text-fig. 16) is reproduced from Weintraub and Price (1947) which probably

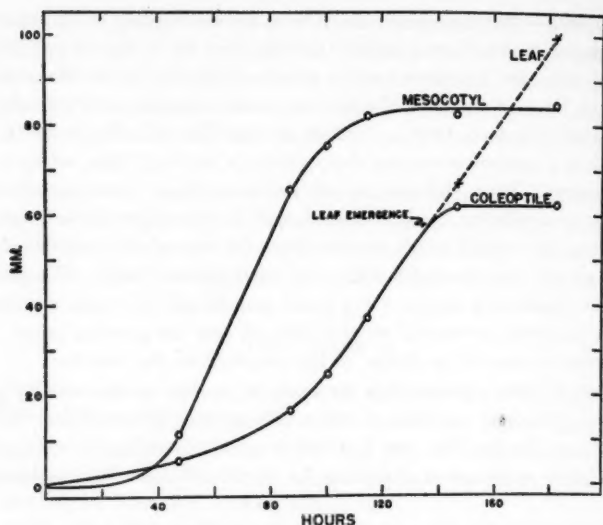


Fig. 16. Growth curves of the parts of a new oat seedling, in darkness at approximately 25° C. (From Weintraub and Price, 1947).

expresses fairly well the relationship of the pre-leaf and its enclosed true leaf. This curve represents the growth of the oat coleoptile and first leaf in the dark. It is observed that both structures have the same growth rate, and also that as soon as coleoptile growth stops, the leaf emerges. One must assume, therefore, that both structures began growing at approximately the same time unless some drastic change of leaf growth rate occurred, which is improbable. While this curve pertains specifically to the oat coleoptile, it undoubtedly applies roughly to the growth of the prophyll and the first leaf of an axillary bluegrass shoot.

It may be interesting to explain the presence of the third curve, labeled "mesocotyl" (text-fig. 16). The mesocotyl is an internode of the oat seedling which elongates upon germination and sends the growing point and the immature coleoptile up toward the soil surface. The curve shows this internode elongating before any of the leaves, which is not in keeping with previous statements to the effect that internodes elongate only after their associated leaf is fully developed. However, McCall (1934) in his examination of the oat seedling has shown that the so-called mesocotyl is the *first* internode and that another very short internode, the second, separates it from the coleoptile which can be thus considered the second leaf. The second internode does not elongate. Since the mesocotyl belongs to the first phytomer, it is under no obligation to wait for the coleoptile to elongate. The leaf of the first phytomer is minute and not readily visible. The basic system of phytomer development thus holds as true in the earliest stages of seedling growth as in more mature plants.

Growth of the Young Tiller.—Table II and text-fig. 15 show very well the interrelations between the parent shoot and the development of intravaginal branches. On a given phytomer the bud does not begin to grow into a tiller until the phytomer leaf has matured its blade and begun its sheath. Then four organs grow at the same time, the main sheath and the next main blade, the prophyll, and the first shoot leaf.

Since the prophyll and the shoot are thus synchronized, succeeding branch shoots are also synchronized. This accounts for the observation that in a sequence of intravaginal shoots on a plant, from the oldest to the youngest each shoot has one less leaf (text-fig. 17). There are exceptions to this of course. No one

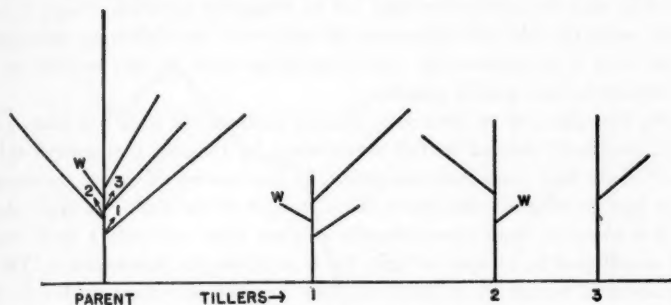


Fig. 17. On a plant which produces numerous tillers, each younger tiller is one leaf behind. W is short winter leaf.

phytomer seems to be wholly compelled to operate strictly in agreement at all times with its neighbors, though for shoots produced during the optimum tillering period in fall, under good conditions, such agreement seems commonly to exist. Under less favorable situations it is only reasonable to expect that a bud might hover between the decision to grow now and become a tiller or wait and grow up to be a rhizome. The indecisive individuals explain transitional types which are not strictly synchronized.

The prophyll may be longer but it is usually shorter than the leaf blade it encloses. In any case, the first sheath raises the first leaf out of the prophyll and exposes it to light. Other leaves of the shoot follow in the usual sequence, and the tiller becomes a new plant. Its own axillary buds can develop into other shoots in the same fall provided shooting starts early enough. Three generations are not uncommon and four or five are possible (pl. 9, fig. 28). Roots grow out from each mature node of the tiller crown and give it some measure of independence. In late spring any spare buds may develop into rhizomes. An inflorescence may appear the first spring though it is usually shorter and bears fewer leaves and spikelets than an inflorescence of the main axis. An intravaginal shoot with as few as two leaves can produce a panicle, while a rhizome with less than seven or eight leaves seldom flowers. This is in agreement with the observations of Cooper

and Saeed (1949) on ryegrass where a minimum of eight leaves are required before the main shoot will flower, while some tillers flower with only a prophyll.

Shoot vs. Leaf Width.—The above facts indicate that the flowering stimulus, once developed, can be transmitted from the main shoot to its tillers. To what extent other aspects of the growth of tiller and main shoot are interrelated is difficult to tell. Von Oettingen (1930), in a study of bluegrass leaf widths, stated that on rhizomes which have turned up there is usually a gradual increase in leaf blade width up to a certain point. Wherever an intravaginal shoot appeared, however, he found the leaf above to be abnormally narrow. This he attributed to a drain on the food resources of the main shoot by the branch. There are several reasons why such an explanation may not be altogether justified, though it is not so much with the idea of disproving his idea that the following discussion is presented as it is to demonstrate how information such as that included in this study may apply to a specific problem.

In the first place, as we have seen, the leaf blade on the main axis above a new tiller has practically reached its full development by the time the prophyll and the first leaf of the tiller start their elongation, so that one would expect any competition for food to influence the sheath above instead of the blade. It might also be added that bluegrass is an extraordinarily efficient plant and only a small amount of leaf would need be exposed to light for it to attain its independence. The enclosing leaves of winter are so short and limp that the new shoot reaches the light very soon after it starts to grow. Likewise, the first leaf is very small and would not consume extensive reserves in reaching its full extension. The efficiency of bluegrass in making maximum growth with a minimum of leaf and minimum consumption of stored carbohydrates or of accumulation of carbohydrates on a minimum of leaf has been suggested by data in Smelow (1937), Klapp (1938), Peterson (1946), and Harrison and Hodgson (1939) among many others.

Von Oettingen himself has indicated that reduced width is not correlated with a reduced number of vascular strands. In tillering varieties of sweet corn it has been shown that so-called suckers contribute to, rather than drain, food supplies of the parent (Jones et al, 1935). The explanation of Von Oettingen's observation is probably much more simple and points out the need for understanding not only the course of anatomical maturation but also the seasonal sequence of development of a plant to which statistical and taxonomic techniques are to be applied. The comparison made by Von Oettingen involved rhizomes which had no shoots and those which had only one or two. As a general rule, any rhizome which appears in fall will develop at least one or two side shoots, but those appearing in winter and spring are not apt to have any such shoots. The plants with branches thus go through a winter, and during that time leaf width of short-leaved plants decreases naturally (text-fig. 18). It is on these one or two late fall and winter phytomers that most of the branch shoots appear, and they are thus automatically associated with narrow leaves. Spring leaves are longer and wider and thus the contrast is accentuated. If, then, plants are later pulled up in summer at random

and the leaf widths examined, the significance of the narrowness of leaves associated with intravaginal shoots is not apparent.

Even the observation of a correlation between shoots and narrow leaves is open to some criticism. According to text-fig. 18, the relationship is actually just the reverse in rank meadow grass, where fall leaves increase in width while shoots increase in number. In grazed grass the early fall leaves increase in width while winter leaves become narrower. Shoots, meanwhile, increase in number all winter long, and virtually every new bud develops into a tiller. Therefore if the shoot had any effect on the leaf width it should show up in the average.

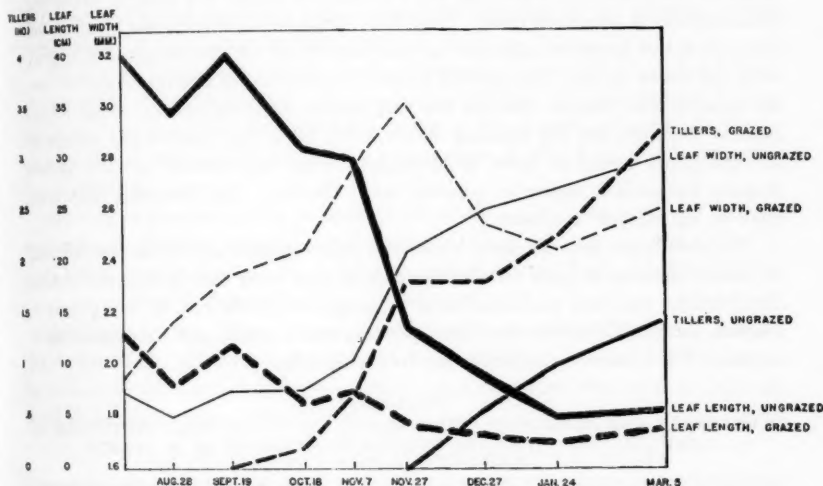


Fig. 18. Relationship of tillering, leaf length, and leaf width in meadow and pasture bluegrass in fall.

There are also indications that the severity of the winter and the seasonal development of available nitrogen in the soil influence the sequence of leaf widths. If the soil is frozen much of the winter, leaves will be deprived of water and will be narrower as a result. In mild winters such as that of 1949-1950, when the leaves were measured (text-fig. 18), very little freezing weather was encountered. One might thus expect that midwinter leaves of bluegrass grown in northern localities would consistently be narrower than those of southern-grown plants.

Shoot vs. Leaf Length.—While the relationship between leaf width and the presence of shoots does not seem to be constant, there is one correlation which seems to be rather consistent under normal cultural conditions: that is, the association of short leaf length with much tillering. This association is suggested in many ways. It is quite noticeable that mowing or grazing rank grass in early fall causes a great increase in the number of tillers. On unmown grass develop-

ment of shoots is weak and delayed until late fall or early winter. This difference is expressed the following spring in a much larger number of panicles in the mown grass (Spencer, 1949) and in the thickening of the early spring stand.

Some preliminary measurements of leaves on plants examined in late spring gave the following results:

Blade length	Number with shoots	Number without shoots
13-30 cm.	3	12
12- 3 cm.	27	5

More detailed data taken on grazed and ungrazed sods in fall and winter are compiled and presented in text-fig. 18, which shows clearly the delay of branching characteristic of ungrazed grass. This delay amounts to nearly two months, and the critical leaf length would seem to be around 10 or 12 cm., which is in keeping with the above figures. On grazed grass, however, leaves average under 12 cm. for most of the summer, but no shooting occurs until September. Leaf length alone is therefore not the deciding factor. We have thus defined the permissive and obligatory limits of shoot development. They can develop as early as late August, but seldom appear in quantity until October. By December they seem more or less obliged to appear.

The association between short blades and intravaginal shoots is further reflected by results obtained in some fertilization experiments made during different seasons. The fertilizer used was undiluted horse urine applied at the rate of two gallons to a square meter. Urine was used because of its quick action and its natural implications. The results are shown in the following table:

TABLE III
LEAF LENGTH AND NUMBER OF INTRAVAGINAL SHOOTS AS RELATED TO TIME OF
FERTILIZATION. (FIGURES REPRESENT AVERAGES OF 10 PLANTS
MEASURED ON JUNE 4, 1949)

Fertilizer applied	Number of branches	Leaf length of last complete leaf (cm.)
Late August	5.8	6.5
Late September	10.0	21.2
Late October	8.1	33.2
Early January	3.7	55.7
Early April	3.1	33.7
Control (no fert.)	3.6	15.0

Plants typical of the above experiment are shown in pl. 9, fig. 29. With a fall application a decided increase in shooting was observed so that in spring a large number of panicles were seen, but the numerous leaves were abnormally short. Winter applications yielded only slight increase in shoots and inflorescences, but the leaf was exceptionally long. The data for August show that again shortness of leaf is not infallibly followed by prolific branching. It emphasizes, instead, that probably no correlation holds true except under specific seasonal and environ-

mental conditions. The rhythm of the plant itself must be considered in interpreting measurements of this sort. In August, day length, soil moisture, and temperature are all quite different from those of September or October, and as already shown the plant is essentially incapable of forming shoots during that period. It is not strange that its response then should differ considerably from that a month or two later. There was little carry-over effect of the August application of urine because of a hot dry period during which much of the nitrogen was apparently lost. The extreme shortness of leaf in the August plants is not readily explainable, except for the possibility that the slight burning effect which the urine had on that occasion may have depleted the plants' reserves at a critical time. It has been observed that very close cutting or stripping of top growth at this period results in weak short-leaved plants.

Tillering in bluegrass has been shown to depend to some extent on day length (Evans, 1949; Harrison, 1934). Temperatures may also be a determining factor, for in the laboratory cultures with baby bottles it was found that while no shoots were produced with a 14-hour day at temperature of 70° F., at 40° numerous shoots appeared.

Shooting is thus seen to be a complicated activity. It depends on day length, temperature, nutrition, stage of development of the plant, and is associated with short leaves, though all short leaves do not produce shoots. Leaf width bears little if any relationship to shooting, except coincidentally.

Death of Shoots.—There is strong evidence that the parent plant may control the destiny of the tiller at certain critical points of development. This begins to be obvious at the time of elongation of the panicle, about the 10th to 20th of April in central Missouri (Table IV).

TABLE IV. DEATH OF INTRAVAGINAL SHOOTS IN SPRING

Date	Number of shoots examined	Number dead	Per cent dead
March 19	12	0	0
April 2	13	0	0
April 17	19	6	32
April 24	15	4	27
May 1	16	2	13
May 7	17	9	33
May 14	16	8	50
May 23	19	8	42
May 31	26	11	42

Dying of tillers is especially evident in rank, sod-bound, nitrogen-deficient grass which has not been grazed or mown, though it is probably also a common event wherever conditions are not ideal.

Death of some branches is a necessity in a sod which maintains a more or less even density from year to year, even though the average number of new vege-

tative shoots per plant is seldom more than two. The main shoot dies after bearing an inflorescence. Of the two tillers, one is generally dead before flowering is completed (Table IV). Perpetuation of the grass through the rest of the season is thus left up to the one remaining intravaginal shoot and whatever rhizomes develop during summer or fall. By early winter, however, practically all the original tillers have died, and it can be seen that maintenance of the population from one year to the next under meadow conditions is primarily dependent on the production of rhizomes. Rhizomes which develop in summer are primarily responsible for the inflorescences of the following year.

That the apparent detrimental effect which blooming has on the tiller may be related to water shortage is suggested by Sharman's statement (1947), that when the apices of the blind shoots (non-blooming tillers) of *Agropyron repens* are dissected during the flowering season they are "pliant and do not cut crisply, as though they were suffering from lack of water." As in bluegrass, these shoots of *Agropyron* generally die before the end of the year. It is also well known that grass crops such as maize require especially large quantities of water during the period of elongation of culms.

It would seem to be to the grazer's advantage to keep these tillers alive since they provide much of the summer's forage. By mowing at the proper time (about the third week in April) and by cutting low enough to catch the flowering head, blooming can be prevented and the vigor of the tillers might well be maintained. Unless these tillers live into the summer there may be a considerable loss of forage or sufficient thinning of the stand to permit invasion by weeds. Mowing at this stage of growth is not common in the United States, but Hamilton (1942) has mentioned that it is a practice on the intensively farmed ryegrass pastures of New Zealand, and suggests that were more power-mowing equipment available it might be profitably practiced more widely. Grazing at the proper time might also be used to serve the same purpose. Ryegrass, as Cooper and Saeed (1949) point out, is more of a problem, for usually a single cutting is not sufficient to prevent later flowering. Since bluegrass can only become "ripe to flower" during winter, one cutting is all that is necessary in that species.

Ahlgren (1938) has made tests simulating three conditions of spring-grazing, the first cutting of bluegrass being made: (1) to a 1½-inch level at a grass height of 4-5 inches; (2) when the head had just appeared; (3) after the head was mature. His data seem to substantiate the above conclusions, for making the cutting at the 4- to 5-inch height for a period of six years gave a progressively greater yield each year. Cutting at the time of appearance of the panicle was also consistently better than cutting at maturity. The data are reproduced below:

The 4- to 5-inch height just about coincides with the period when the panicle is starting to elongate. The specific time for mowing to best advantage can be determined by examining the heights of a few panicles while they are within the sheaths to see if the mower will cut them. It is quite possible that one of the more

subtle benefits of grazing a pasture involves the prevention of heading at an early stage, and thus the encouragement of the tillers which must take the plant through the summer.

TABLE V

PERCENTAGE YIELD OF KENTUCKY BLUEGRASS FROM PLATS GIVEN VARIOUS CUTTING AND FERTILIZATION TREATMENTS. (FROM AHLGREN, 1938)

Year	Complete fertilization			No fertilization		
	4-5 inches	Early heading	Fully headed to mature	4-5 inches	Early heading	Fully headed to mature
	%	%	%	%	%	%
1932	79	123	100	71	93	100
1933	92	97	100	74	81	100
1934	113	103	100	108	101	100
1935	108.2	108.2	100	118.8	110.8	100
1936	143.6	105.4	100	189.8	136.7	100

THE FLOWERING SHOOT

Purpose and Design.—Bluegrass must be appreciated more for the delicate and effective way in which it presents its small flowers to the wind than for the beauty of the individual flower. There may be from 100 to 1000 flowers, or *florets* as they are called in grasses, on each flowering shoot. Considering that the plant has only the phytomer to build with, it does a very efficient job of display. By elimination or reduction of all unnecessary structures including blades, sheaths, roots, and some buds, a flowering shoot of quite simple design is achieved. This shoot consists of a main stem or *culm* which holds a branched pyramidal inflorescence or *panicle* well above the ground (text-figs. 3 and 20). Clusters of florets (called spikelets) depend from the tips of the panicle branches. The average culm is merely a portion of the vegetative axis which has been obliged, because of the initiation of an inflorescence at its growing point, to follow a course of development different from that of non-flowering shoots. It is distinctive chiefly in having long internodes, reduced leaves, no buds or roots, and a hollow stem, all of which indicate the strong economies of material put into force when the plant is called upon to flower.

The average culm consists of a series of 3, 4, or 5 phytomers, with each higher one being less like the normal vegetative ones at the base of the plant. For convenience the standard number of phytomers will be considered as 4, and will be numbered from the lowest, least elongate (1) up to the highest and longest (4). Actually there is no specific phytomer at the base which one can designate as belonging to the flowering shoot rather than to the vegetative shoot from which

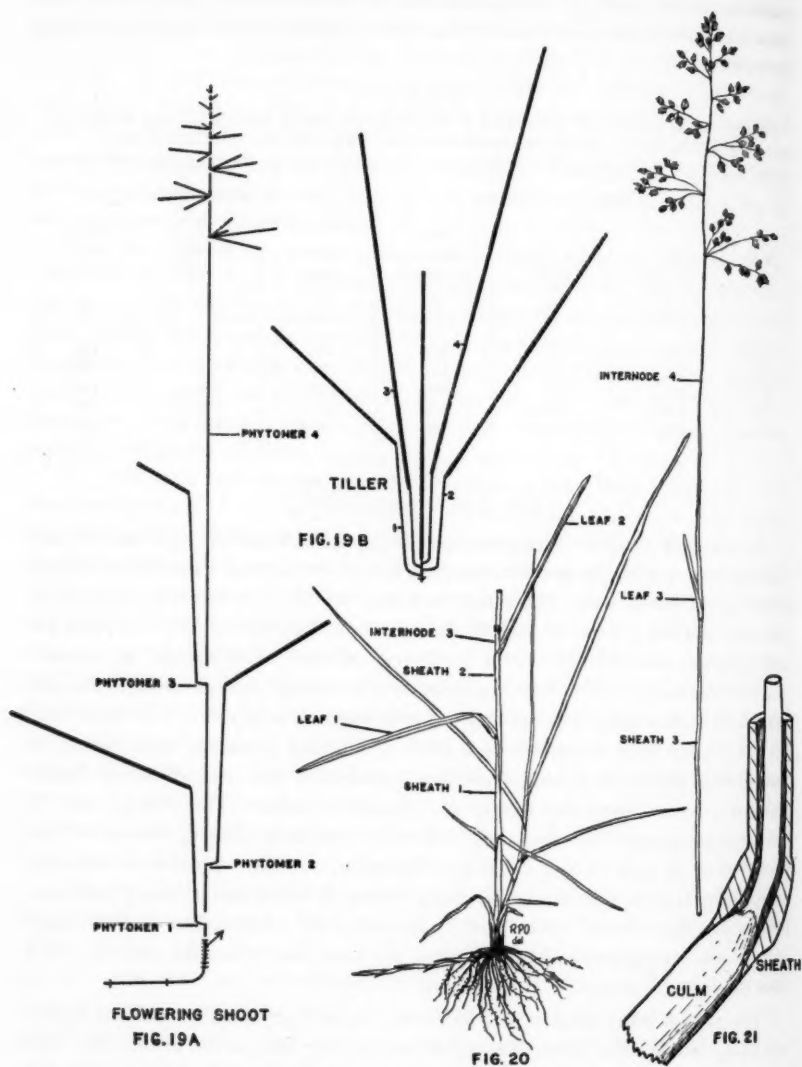


Fig. 19. Diagram of a typical flowering shoot (A), and one of its tillers (B).

Fig. 20. Bluegrass plant from an old meadow showing an average flowering shoot.

Fig. 21. A fallen flowering shoot is straightened by the development of tissue on the lower side of the enclosing sheath.

it springs, for the transition is not always abrupt. Each of these culm phytomers is a distinctive combination of different internode, blade, and sheath lengths (text-fig. 19A). In an old unmowed, ungrazed, unfertilized, unirrigated, unshaded stand of Missouri bluegrass the lengths of successive internodes will increase toward the panicle in a rough ratio of 1, 4, 12, 30. The panicle on top would then be about 9 cm. Each of these internodes, except the last, bears a sheath at its top which in turn bears a blade. The average sheath lengths in centimeters would be about 9, 12, 13 and 0. The leaf blade lengths are in reverse order to the internodes for they average 13, 9, 4 and 0. We thus can draw the following thumbnail arithmetical sketch of the flowering shoot:

TABLE VI
COMPARISON OF LENGTHS (IN CM.) OF FOUR SUCCESSIVE *CULM* PHYTOMERS
WITH THOSE ON A SUCCESSION OF FOUR *VEGETATIVE* PHYTOMERS ON
ASSOCIATED TILLERS. (SEE TEXT-FIG. 19 A & B)

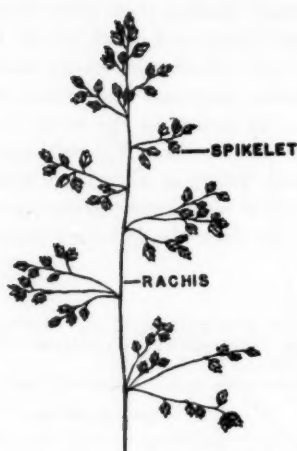
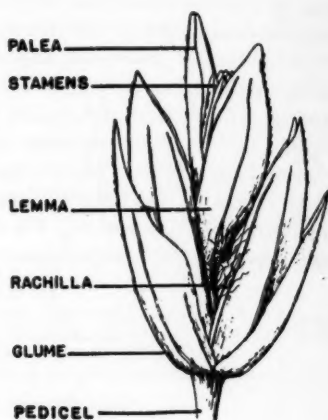
	Culm phytomer					Vegetative phytomer			
	1	2	3	4	Pan- icle	1	2	3	4
Internodes	1	4	12	30	9	—*	—	—	—
Sheaths	9	12	13	0	0	8	6	5	6
Blades	13	9	4	0	0	12	20	24	30
Total leaf	22	21	17	0	0	20	26	29	36
Date leaf completed	Apr. 12	Apr. 17	Apr. 26			Apr. 12	Apr. 26	May 16	June 15

* Vegetative internodes too small to be measured.

The last sheath immediately below the panicle may appear as a small hook or scale at the top of the last phytomer. Rarely a complete leaf may be found. These figures give only a general picture of the culm, and it is not intended to suggest that they pertain to other strains or plants from other habitats. The first phytomer is seen to have a very short internode and a long leaf blade while the last phytomer has a long internode and no leaf at all. The first leaf is not greatly different so far as blade and sheath length are concerned from its vegetative contemporaries (text-fig. 19B, No. 1). With the second blade, however, the influence of the developing panicle is evident, for comparable vegetative blades average 10 cm. longer than those on flowering shoots.

Culm leaves are consistently broader than the contemporary leaves of associated vegetative shoots. Thus measurements of the last leaves on 48 plants, 24 with inflorescences and 24 without, showed on April 21 average widths of 3.4 and 2.3 mm. respectively. On May 1, after the last culm leaf had appeared the difference was 2.7 and 2.3 respectively. This indicates that the *last* culm leaf is less wide than its predecessors. In general, there is little difference in the width of the first two culm leaves.

The internodes of the bluegrass culm are rather delicate structures which would soon fall to the ground were they not partly encased by strengthening sheaths.

Fig. 22. A bluegrass panicle, $\times 4$.Fig. 23. A bluegrass spikelet, $\times 16$.

The lowest two internodes are usually completely hidden from view while the third generally shows only a few centimeters at the top. The last internode is sheathed about half way up. The degree of overlap varies radically from plant to plant.

In case the bluegrass culm, while elongating, happens to fall to the ground as a result of wind, rain, or trampling, a rapid reaction takes place in the vicinity of one or more of the nodes causing development of tissue on the lower side of the culm which gradually restores at least a part of its perpendicularity. On close examination it will be found that in bluegrass the actual growth and straightening process depends more on the basal part of the sheath than on the internode (text-fig. 21). This sheath builds up a wedge-shaped accumulation of tissue around its lower side, which as it bends up, forces the delicate culm within to raise also. Arber (1934) states that in other species of grass such straightening may involve only the sheath, as in bluegrass, or both sheath and internode, or internode alone. The bluegrass internode, whether on the culm or the rhizome, apparently has very little to say about what position it will assume.

The Panicle.—At the summit of the culm is the panicle or inflorescence (text-fig. 22). The branches of this panicle, which arise at nodes, are grouped together in successive fan-shaped tiers inserted alternately on the panicle axis. Since the branches of the lower tiers are longer than those of the upper ones the outline of the inflorescence is somewhat pyramidal. There are from three to five branches at each of the lower three or four nodes, and these are almost perpendicular to the main axis at flowering time though in some strains they may droop or be appressed to the panicle axis. The spikelets, or flower clusters of the grass, are borne at the tips of these branches and of their subsidiaries.

The panicle axis, or *rachis* as it is sometimes called, is a continuation of the culm. It is composed of some eight or more internodes, only the lower ones being very prominent. This contrasts with the culm internodes which decrease in length toward the base of the plant. There are no leaves on the rachis phytomers.

Beginnings of the Flowering Shoot.—A flowering shoot is a sudden, striking thing and seems so different that it sometimes prevents us from understanding its relation to the course of development in the rest of the plant. In bluegrass the initiation of the flower takes place in the cold weather of late fall and early winter, and thus development is slow and goes unnoticed. In spite of its early start, bluegrass does not display its flowers until mid-May in Missouri. Cold weather and short days have no magic in themselves, and can work only through the physiological systems of the plant. Under fall conditions it has been shown (Buckner and Henry, 1945; Peterson, 1946) that bluegrass carbohydrate reserves rapidly reach a peak. In general, such accumulation of carbohydrates seems to be one of the significant factors leading to the "ripe to flower" condition in grasses. That other systems play a part goes without saying, but no effort will be made here to fathom the chemical complexities associated with the inception of flowering shoots.

To trace the development of a vegetative shoot into an inflorescence we shall have to go back to the growing point, for that is the beginning of everything. Musgrave (1940), Nishimura (1923), and Evans (1949) have given good accounts of this process. The following description attempts to synthesize the work of these three authors.

The vegetative growing point runs on a rather close margin. It commonly has only three or four phytomer primordia differentiated and available for use (see pl. 5, fig. 13). As the plant approaches fall, however, either the phytomer organs differentiate less rapidly, or else new primordia are cut off from the growing point at an increasing rate, or both, for incipient phytomers begin to accumulate and as a result the blunt rounded vegetative growing tip of the youthful shoot becomes a longer, rather conical, wrinkled, translucent point (pl. 8A). This is a tendency which precedes inflorescence development in practically all grasses, although the number of phytomers accumulated on the point and its actual length may vary greatly with different species.

Protuberances Appear.—The lower, old phytomers of this new cone appear normal enough, and bear the usual leaf primordium at their upper end, but toward the point, on the younger primordia, there may be only a faint ridge or no sign of a potential leaf. Then something happens. The deadline is up, and all phytomers which have not formed leaf primordia are obliged to get along without them, for the reproductive phase has begun. The first visible sign of this event on the growing point is the appearance of small knobby protuberances which, though arising in a similar alternate manner, are obviously different in origin from the crescentic ridges from which leaves arise (text-fig. 24A; pl. 8B). These shining protuberances appear first on those phytomers which have only the faintest trace of a leaf ridge, then soon both *below* and *above*. The protuberance is a rather

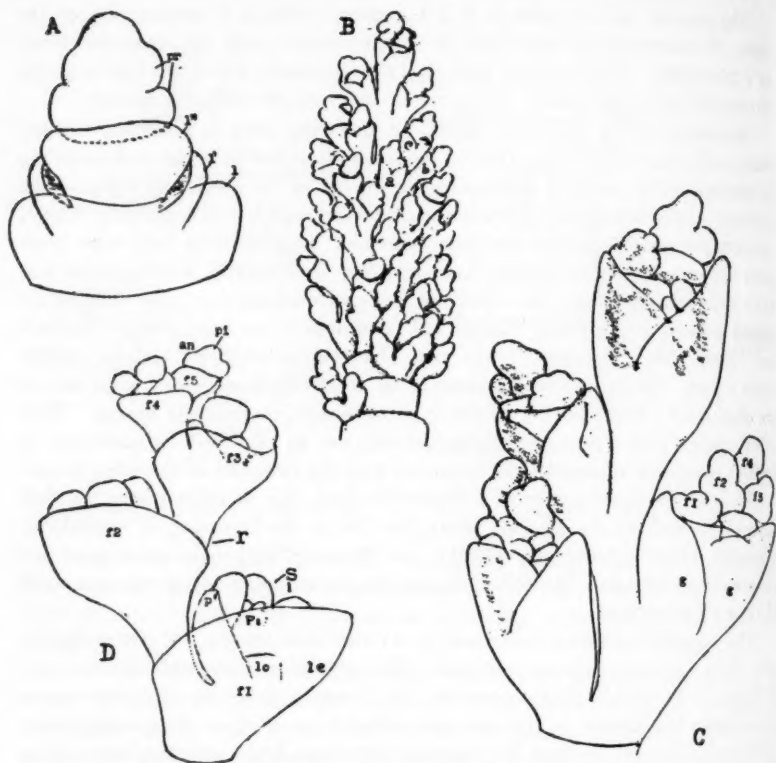


Fig. 24. Drawings from Nishimura (1923) showing details of panicle and spikelet development: A, the elongate growing point which anticipates panicle development; B, small ridges begin to appear on the advanced protuberances and foretell development of glumes; C, a panicle branch holding several developing spikelets; D, a much-enlarged individual spikelet with glumes removed and showing beginning of development of florets and reproductive parts; *pr*, protuberance; *l*, *l'*, *l''*, successive leaf primordia; *g*, glume; *f1*, *f2*, etc., successive florets; *an*, stamen primordium; *pi*, pistil primordium; *r*, rachilla; *p'*, palea; *lo*, lodicule; *s*, stamen.

unique development for, although it obviously represents a branch of the main axis, it is the only time during the growth of a grass that a growing point is not encased in its own sheathing cone of leaves. Here is a phytomer which consists of nothing but stem. Through continued cell division it grows very slowly, almost as though it were a root. The one phytomeric function which it seems to retain is the ability to branch. Thus after about a month secondary protuberances arise (pl. 8C), and in another month tertiary ones appear. By this time most of the winter has passed, and in late March the growing point may still be only about 1.5 mm. long and yet will contain practically all the cells necessary to build the entire skeleton of the mature panicle.

The Development of Spikelets.—In April on all the naked ends of protuberances of all orders small crescentic ridges begin to appear (text-fig. 24B). Just as in

the main vegetative point, these ridges are alternately arranged and later develop into minute leaf-like structures. Thus the conventional phytomer consisting of a leaf and an internode is reestablished. This is the beginning of the bluegrass spikelet, or flower cluster (pl. 8D; text-fig. 24C). The first signs of spikelet development appear on those protuberances located somewhere between the middle and upper third of the panicle, and the spikelets at the tips of the *main* branches develop before those on subsidiary branches.

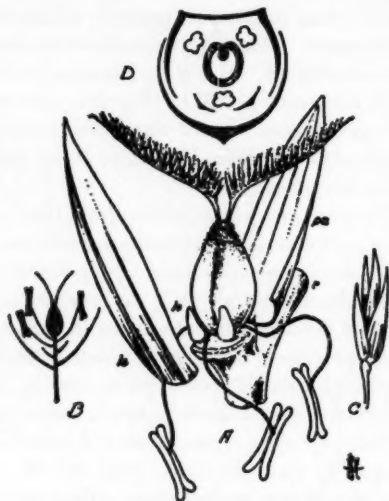
The first two leaf-like structures which develop from these primordia are called *glumes*. They are only 2 or 3 mm. in length when mature, and completely enclose the growing point and its developing structures. Once conceived, the two glumes elongate more or less simultaneously, which is not exactly in keeping with the usual sequence of phytomer development. As shown in text-fig. 26, the last two blades and then the last two sheaths of the culm elongate simultaneously, so that apparently when the growing point is going into or coming out of the phase of panicle formation the normal sequence of elongation is somewhat altered.

Before the glumes close over the growing point a series of 3-5 phytomers with leaf primordia have begun to form (text-fig. 24C; pl. 8E). These primordia elongate gradually after the glumes enclose them. They are called *lemmas*, and they are distinguished from the lower glumes because they bear, in their axils, an axillary bud which will soon develop into that long-awaited-for phenomenon, the *floret* (text-fig. 24D).⁴ Differentiation of successive lemmas and florets progresses from the base of the spikelet toward the tip.

As with most axillary buds, the first structure produced from the floret bud is a membranous, two-veined, compressed sheath-like organ which, though not called a prophyll any longer, very much resembles one. It is dignified by the name *palea*. The growing point of the floret bud (text-fig. 24D), then proceeds with the differentiation of the critical flower parts, producing in turn three stamens from small papillae just below the growing point, the pistil from a crescentic protuberance very much resembling a leaf primordium, and finally the two styles and stigmas from papillae on the pistil (text-fig. 25). The ovule or egg sac, which is perhaps the final leaf primordium, remains short inside the pistil after that structure has closed around it. Within it will develop the egg cell, which would appear to be the arrested growing point.

From four to seven phytomers are ordinarily found in a bluegrass spikelet. Their leaves are the glumes and lemmas, their axillary buds are the florets, and their minute internodes join together to form the spikelet axis or rachilla (text-fig. 25). The transition toward termination of the growth of this axis is usually expressed in the form of a final much-reduced phytomer which consists of a fragile internode and a minute lemma, the so-called sterile floret.

⁴By following the phytomer concept to the end and assuming that the glumes are homologous with sheaths or blades, we should, in reality, recognize the first three leaves (two glumes and the first lemma) as glumes instead of just the first two, since the first floret is a bud at the base of the fourth spikelet phytomer, and thus belongs to the fourth leaf, not the third, which is therefore "sterile." This is a technicality of no great importance to the matter at hand, and might cause considerable confusion among grass taxonomists. That there are no hard-and-fast rules in this respect is illustrated by the observations of Sharman (1947) that florets are sometimes found in the axils of the glumes.



A, flower of a grass (schematic); lo, lodicules; r, rachilla; lo, lemma; pa, palea; B, longitudinal diagram of flower; C, spikelet; D, floral diagram.

Fig. 25. A diagrammatic sketch of a typical grass flower. (From fig. 429, on p. 627, of Johnson's "Taxonomy of the Flowering Plants," 1931. Reproduced by permission of the Century Co., Publishers).

Elongation of Panicle and Internodes.—As the process of spikelet differentiation proceeds in early April, it seems to send a pulse of life down through all the phytomers which have been biding their time since being inhibited when the proliferating urge assumed control months before. Their internodes begin to elongate. The actual processes involved in this revival of growth are shown in text-fig. 26. The initial quickening is limited to the panicle proper. Growth is slow at first, less than 1 cm. between March 27 and April 12, then it increases rapidly during the next ten days to full length. It may not be altogether a coincidence that this panicle elongation comes immediately after the first and second leaves of the culm have matured. It suggests that some inhibition may be involved.

Not until the panicle has reached its mature length do the internodes of the culm begin to elongate to any extent. An exception to this is the first short internode, which begins to lengthen several weeks before the panicle matures. This course of growth seems slightly different from that characteristic of wheat as shown in text-fig. 6. In wheat the growing point at the beginning of the protuberance stage has had more phytomers and culm development is more drawn out and deliberate, with each successive internode behaving as an individual. The result is a culm with more joints of more nearly equal length. Maize is a more extreme example of this same situation. Bluegrass with its short growing point presents only four internodes, only three of which reach any considerable length.

It is a common observation that in wheat, corn (Sharman, 1942), and rye (Prat, 1935) the last two internodes elongate at the same time. Prat attributed this to the fact that there is no leaf on the last phytomer, therefore, the internode does not have to wait to begin its growth. The fact that in the bluegrass strain examined here the last *three* internodes grow at the same time is probably related to the absence of the last blade and the shortness of the third one.

Culm Leaves.—While it is usually considered that the bluegrass plant lies dormant during winter except for inflorescence initiation, it is actually producing a certain amount of leaf growth. On shoots destined to flower, no new leaf primordia are produced once proliferation takes place, but those primordia already completely formed do follow a normal course of development within the limits of environmental factors. The number of leaves which thus develop during the coldest weather is usually only two or three and these are very short (text-fig 26WB). The internodes below these winter leaves do not elongate, for they are apparently mature by the time spikelets begin to differentiate in spring. These leaves differ little, if at all, from comparable leaves on vegetative plants or on tillers of the same plant.

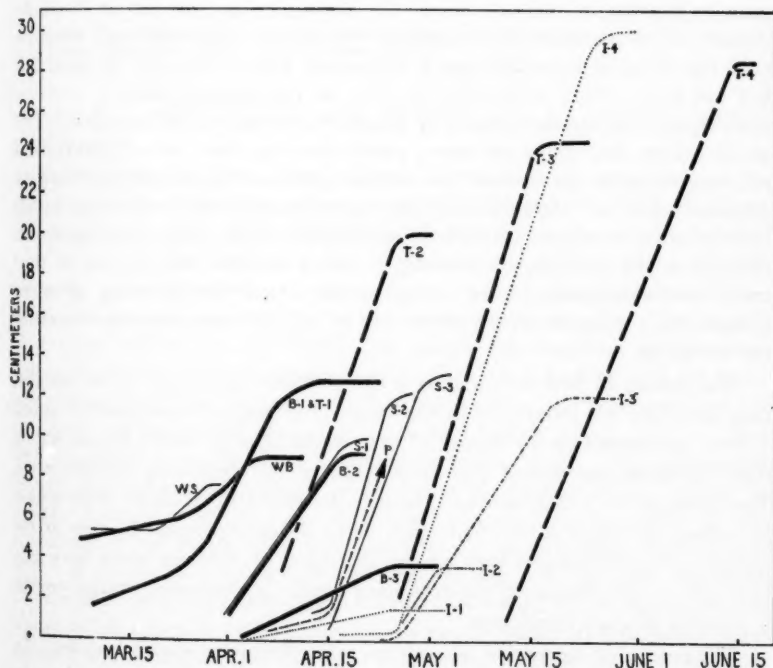


Fig. 26. Curves of growth made by various organs of meadow bluegrass during the period of flower-shoot development in spring.

With the approach of warmer weather in late March leaf growth receives an impetus and new leaves grow longer. The last true winter leaf and the first culm blade apparently respond, rather abruptly, to the rise in temperature. (See sheath WS and blade WB and B-1 in text-fig. 26.) The first blade on the culm continues elongating. By early April it is joined by *leaf blades 2 and 3* and *sheath 1*, which elongate at the same time. When these mature, *sheaths 2 and 3* and the panicle elongate almost simultaneously. Immediately upon their maturation, *internodes 2, 3, and 4* begin to grow. This rush of growth is in decided contrast to the deliberate growth of phytomers on vegetative shoots of the same plant where only one blade and one sheath elongate at the same time and the internodes do not elongate at all. This speeding up of the development of phytomers immediately below the inflorescence has been noticed by Sharman in maize (1942) and in quack grass (1947) and is suggested by data of Prat (1935) for rye. This is one of the factors involved in the rapid appearance, in spring, of a large number of leaves in a very short time. The more flower shoots there are the more vigorous this spring flush will be.

There is an interesting contrast between culm and vegetative leaves with respect to final length and rate of growth. Up until about the last of March the growth rate of the two types of leaves is very similar. After that each successive culm leaf elongates less rapidly and is successively shorter (text-fig. 26, leaves B-1, B-2 and B-3). Tiller leaves (T-1 to T-4), on the contrary, elongate somewhat more rapidly, and become successively longer even though on the same plant. This would suggest that if the developing panicle has any effect on leaf growth, it is not transmitted to the leaves of intravaginal shoots as the stimulus for flowering apparently can be. More probably, the shortening of culm leaves is not an inhibitory effect at all, but dates back to the time when the growing point first changed in the direction of flowering. Leaf primordia were stopped in their tracks and consequently when an opportunity came the following spring to elongate there were successively fewer cells in each younger primordium available for elongation.

The absence of buds on the culm is also probably due in part to the fact that their formation was interrupted by the inception of panicle development. Sharman (1947) commented on the absence of buds on the culm of certain species, stating that microdissection showed that early stages of bud formation did take place. The failure of the bud to develop further he attributed to the effect of elongation in pulling the tissues of the bud apart. This seems improbable in view of the presence of well-developed buds on the phytomers of rhizomes which have long internodes. The influence of the developing panicle in suppressing further growth is probably of more significance.

The reason for suppression of roots on culm phytomers is even less clear. In part, it may merely be that the culm internodes do not come close enough to an adequate rooting medium. Roots have been seen on culm phytomers as far ad-

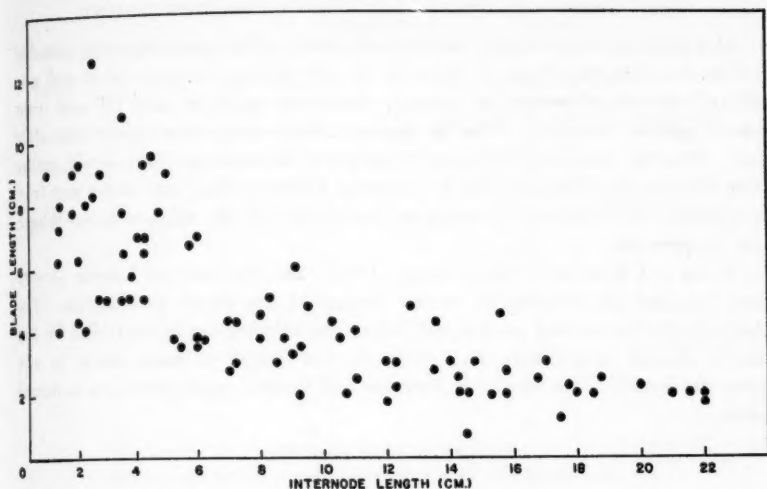


Fig. 27. The relationship between length of phytomer internode and phytomer leaf on the culm of bluegrass. Plants were from various meadow habitats.

vanced as No. 3, under conditions where the nodal region was exposed to moisture and darkness.

The relationship of short leaves and long internodes in the upper part of the culm is apparently more than mere coincidence. Although the shortness of the leaf may be explained on a historical basis, the long internode probably involves other factors. It has been mentioned in connection with the rhizome that the internodes of phytomers whose leaves turn up and reach the light are inhibited. If the leaf does not reach the light then the internode elongates. Many other observations indicate that the bright light inhibits the elongation of internodes, while in the dark or shade elongation can take place. It is probable that the shortness of the culm leaves reduces their inhibiting action at the same time that the developing inflorescence is producing auxin in quantity (Pratt, 1935). Thus both conditions appear to favor increased internode length. The relationship between leaf and internode length on the culms of bluegrass from a variety of habitats is shown in text-fig. 27. As further evidence for the validity of this relationship, it has already been mentioned that the last internode, devoid of any leaf, is by far the longest. Also suggestive is the fact that very little elongation of the second, third, and fourth internodes takes place until the last leaf has reached almost its full extension. Unfortunately, the panicle reaches its final length about the same time, so that there is no way of determining which is the more significant releasing factor.

LEAF GROWTH IN RELATION TO SEASON AND ENVIRONMENT

Day Length, Temperature, and Growth Rate.—The casual observer probably realizes that bluegrass begins to green up in early spring, blooms in May, and gets tall and somewhat brownish in summer, then greens again in early fall and turns brown again in December. This sequence of events seems quite regular year after year. Weather variations induce only moderate fluctuations. One would gather from this that the bluegrass plant has a way of knowing what time of the year it is. Apparently that knowledge is conveyed largely through the medium of day length and temperature.

Evans and Watkins (1939), Evans (1949), and Peterson and Loomis (1949) have described the influence of various changes of day length on bluegrass. The chief conclusions reached are that leaf length and tillering can be controlled by day length, though temperature may affect the leaf length to some extent at any given day length. The results of Peterson and Loomis' experiments are indicated below:

AVERAGE LEAF LENGTHS

Temperature	Day length	
	11 hrs.	19 hrs.
56°–65° F.	9 cm.	15 cm.
61°–75° F.	16 cm.	25 cm.

Day length has been widely studied because its control is so easy under experimental conditions, but it is only one factor among many which affect the efficiency and consequently the behaviour of bluegrass. Over its full range, temperature can exert just as profound an influence. Thus Darrow (1939) has found that "plants grown at temperatures of 59° F., 77° F., and 95° F. produced at 59° a tall succulent bushy top growth with many leaves and at 95° an erect, non-succulent, short top growth with few leaves." Brown (1939) found that under controlled conditions maximum top growth was produced at temperatures between 80 and 90° F. when plants were clipped monthly. He also found that 50 degrees was the critical mean below which very little top growth took place in established sod, but that in new seedlings production was large at an average soil temperature of only 44° F.

In the series of experiments where bluegrass was grown in baby-bottles, the plants were first placed under temperatures ranging from 70° to 75° F. They were later moved to a room kept at 40° F. In the beginning the day length was 14 hours; the humidity was not controlled. Measurements of the growth of individual leaves were made weekly. Average growth rates and leaf lengths are recorded in Table VII.

TABLE VII

Month	Period	Growth per day in cm.	Length of youngest mature leaf in cm. (Average of 12 plants for two periods)	
Nov.	25-30	1.7 }	7.5 }	
	30- 7	2.43 }		
Dec.	7-15	.94 }	15.0 }	14 hrs at 70° F. Av. = 1.78 cm.
	15-25	1.88 }		
Jan.	25- 3	2.07 }	27.0 }	
	3-12	1.64 }		
Feb.	12- 3	.38 }	23.0 }	14 hrs. at 40° F. Av. = .42 cm.
	3- 9	.67 }		
	9-16	.48 }	25.5 }	
	16-22	.34 }		
Mar.	22- 1	.17 }	15.0 }	
	1-15	.47 }		
	15-22	.43 }	9.0 }	12 hrs. at 40° F. Av. = .34 cm.
	22-29	.35 }		
Apr.	29- 5	.25 }	7.9 }	
	5-12	.20 }		
	12-19	1.07	8.2	Temperature up to 70° F. on the 17th

It can be seen that the growth rate became much slower and the leaves gradually much shorter after the plants were placed under the low temperatures. In general, the growing period of a given leaf remained about the same and consequently initiation of new leaves was not greatly retarded. Tillers were not found on any of the plants while they were kept at the high temperatures, but when plants were transferred to low temperatures tillers soon appeared and the leaves became a deeper green. These are changes very similar to those occasioned by growing bluegrass under long and then short day-lengths. Five weeks before the end of the experiment the day length was changed to 12 hours while the temperature remained at 40° F. This change had only a slight effect on succeeding growth rates. During the final week, through failure of the cooling equipment, the temperature went up to 70° F., and did not come down for several days. This resulted in a striking increase in growth rate for that week.

Growth Rates in the Field.—Approximate growth rates of bluegrass leaves under natural conditions throughout the year were calculated from two sources of data. For vegetative leaves appearing in March, April, and May, data collected in connection with the development of the tillers on the flowering shoot have been used. Since all tillers produce very short winter leaves, and then begin with surprising coordination to produce longer spring leaves about the same time, and at the same rate, successive leaves fall into definite length classes which remain fairly distinct for the first 4 or 5 leaves of new growth. It is from averages of 10 leaves of the same class that the curves are made. Dissection of the shoot was

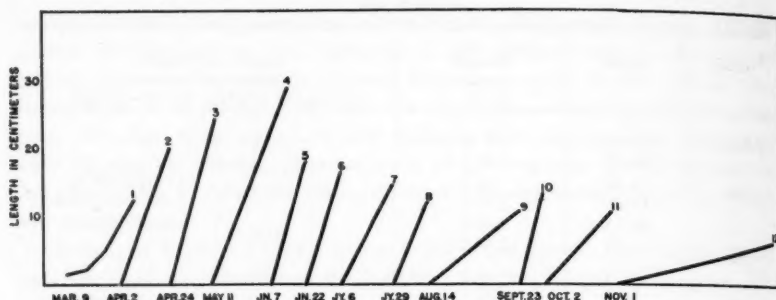


Fig. 28. Growth rates of bluegrass leaves at various times of the year. (Data for leaves 5-12 from Evans, 1949).

necessary in order to measure growth of the young leaves. This method has the advantage over measurement of individual leaves on the same plant, that curves on the entire leaf can be obtained (text-fig. 28, leaves 1-4).

Growth rates for summer and fall leaves (text-fig. 28, leaves 5-12) were drawn from data in Evans (1949). He recorded the date on which each new leaf appeared above the previous sheath on three individual plants. Each of these plants happened to produce 14 leaves during a period of one year so that an average date of appearance could be figured, and from that the interval between the appearance of successive leaves. This recorded interval was not the elongating period of a specific leaf, however, because the first observation that a leaf was growing came after it had already arisen from the growing point and extended itself up through the previous sheath *past* the ligule. About the first fifth of the growth of the blade thus takes place before its existence is recognized. The remaining $\frac{4}{5}$ then goes on to mature. Then there is a delay until the next leaf is recorded, because it has to make the $\frac{1}{5}$ of its growth up through the sheaths just as did the previous leaf. This growth begins when the previous blade matures. Not until the new leaf is exerted does the interval recorded by Evans end. His average interval between the appearance of each new leaf is therefore a composite figure, and instead of pertaining to the whole growth of one leaf it includes $\frac{4}{5}$ of the growth of one blade and $\frac{1}{5}$ of the growth of the succeeding blade. The exact proportions will vary somewhat with variation in sheath and blade length.

Evans has included the average final length of each blade in his data. If we use this information carefully we can arrive at an approximate blade growth rate for the intervals of time between leaf appearance. The recorded interval pertains to parts of two blades, $\frac{4}{5}$ of one, $\frac{1}{5}$ of the next, but the recorded lengths are for one specific leaf. If we take $\frac{4}{5}$ of the length of one leaf and $\frac{1}{5}$ of the length of the next we shall have the actual growth which occurred during a known period

of time and therefore be able to compute a growth rate. This has been done for the summer and fall leaves measured by Evans, and these rates are plotted in text-fig. 28, leaves 5-10. Since the fall leaf blades are proportionately shorter than their enclosing sheaths, the ratio of observed to hidden growth would change, and would be closer to $\frac{3}{4}$ visible and $\frac{1}{4}$ within the sheath. This correction has been applied to the last two leaves.

The following shows the way in which these rates were computed: If we assume that one leaf blade when full grown was 5 inches and the next one 3 inches and the time interval between the appearance of each one at the orifice of the sheath was 10 days, the actual growth during that time must have been $\frac{4}{5}$ of 5 inches (4 inches) plus $\frac{1}{5}$ of 3 inches (.6 inches). Total growth would be 4.6 inches in a period of 10 days, which is a rate of .46 inches per day. There will always be some error involved in such a method but the results are so compatible between leaves measured for this study and those measured by Evans that they are considered to be reasonably accurate for the present purpose. They do not agree with the data obtained in the nutrient solution experiments, where the growth rate was somewhat more than twice the natural rate at comparable temperatures. This discrepancy is probably related to the fairly high nitrogen concentration in the nutrient plus the low intensity of the light source. The complete data of text-fig. 28 do not necessarily hold for any other localities than those where the measured plants grew (Missouri and Ohio) nor to any other years than 1939 and 1949.

Periods of Rapid Growth.—Growth rate is slow in late fall, very slow in mid-winter, and sometimes rather rapid, sometimes slow in mid-summer. Most rapid growth takes place in early spring and in early fall. The spring and fall seasons have much in common for they represent a time of vigorous growth at the expense of the plant's reserves. It was first realized how definite and how similar these two periods were when rhizomes were being collected for the culture experiments described in an earlier section. Rhizomes needed in early October and March and April could never be found. They had all turned up in a flush of green growth which had involved the whole plant. At such times there is a tendency for sods to weaken and fall apart as the reserves are drawn out of old rhizomes and roots. New roots develop rapidly at these times and are short, thick, and white, in contrast to the long, thin, brownish ones of summer.

The period of rapid growth in the spring lasts from March to late April, while the fall rush is limited to a few weeks and depends to a great extent on when fall rains come. Recovery in each case is marked by the beginning of new rhizome production, but, as indicated elsewhere, the late fall rhizomes are shorter than those of summer. Though these periods have much in common, they are necessarily different, for while the carbohydrate reserves of the spring plant are greater to begin with, the progressive increase in day length and higher temperatures, together with a supply of nitrogen accumulated in the soil during cool periods, favors a prolonged period of rapid growth. During fall, on the other hand, reserves are

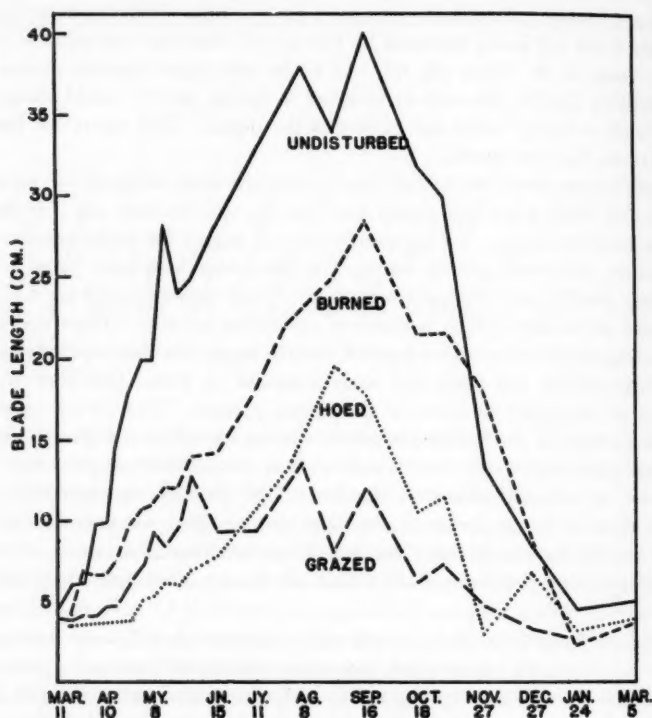


Fig. 29. Prevailing leaf-length through a period of a year under four conditions. Undisturbed grass was in an old meadow. A plot of this grass was burned in early February. Another plot was cleaned of all surface material with a sharp hoe at the same time of year. The grazed grass was in a heavily grazed barnyard area immediately adjacent to the meadow.

low following the heat of midsummer, and day length and temperatures favor a rapid accumulation of carbohydrates which is associated with slow growth. Also during summer there is apt to be considerably less accumulation of nitrogen in the soil due to bacterial fixation.

In addition to day length and temperature, there are other factors which exert considerable influence on leaf growth, either directly or indirectly. Shade increases leaf length (Watkins, 1940), though not indefinitely, since increase in length ultimately depends on amount of reserves available. Nitrogen fertilization makes leaves longer, the extent of lengthening depending on a complex of factors, among them especially time of application, type of nitrate ion (NH_4 or NO_3) and prevailing pH of the growing medium (Darrow, 1939).

Availability of water plays a part, especially in fall and winter. It has been mentioned that plants growing in soils which are prevented from freezing in winter but which are provided with adequate moisture produce very vigorous thick

rhizomes. Plants arising from these rhizomes develop remarkably fast in spring and produce exceptionally vigorous and tall plants. The relationship between fall mowing and grazing and the production of many tillers and consequent shortening of leaves has been discussed elsewhere. Denudation of soil during the period of late winter by skinning all grass from the surface of the frozen soil has been found to have a very strong effect on resulting growth of grass plants. Throughout the succeeding year leaves remain short and narrow, and lack the necessary vigor to compete with weeds. Recovery of such skinned plots is very slow. A similar effect results from skinning in August.

In text-fig. 29 a complete record of bluegrass leaf lengths throughout the year in several habitats is presented. The leaf measured was the last mature one on any given date, and 10 individual leaves were measured in each habitat. A certain amount of lag existed between the actual time of leaf growth and the time when the leaf became mature enough to measure, so that the curves do not express exactly the correlation with day length and temperature that they should. They serve, however, to give comparative results and to show the pattern of effective leaf length at any time of year.

Text-figure 28 gives a rough idea of the number of leaves produced during a year, though some allowance must be made for the fact that one or two winter leaves are not included. Leaf production varied from one every 10 or 14 days in fall and spring to one every 6 to 10 weeks in late fall and winter. Leaf production varies greatly with habitat. On a group of plants from different locations examined at the end of August, 1949, the number of leaves produced above the last intravaginal shoot of the previous winter was as follows:

TABLE VIII
NUMBER OF LEAVES PRODUCED ON PLANTS FROM VARIOUS HABITATS, COUNTED FROM LAST INTRAVAGINAL SHOOT TO LAST MATURE LEAF ON AUGUST 30, 1949

Closely grazed	Old meadow	Dry sterile meadow	Dry shady hill
11	10	9	5
10	11	9	6
10	12	7	5
11	7	8	5
14	9	8	5
16	9	8	6
10	9	8	5
12	12	10	7
12	14	10	5
10	9	9	6
Av. 11.6	10.2	8.6	5.5

Watkins (1940) has indicated that nitrogen fertilization increases the rate of leaf initiation in *Bromus inermis*.

The number of leaves which are green at any one time also varies. Thus, on March 8, 1949, plants growing in a seepy place showed development of 4 or 5 green

winter leaves while on adjacent pasture areas where the ground had remained frozen and dry most of the winter hardly any shoots had more than 2 green leaves. Evans' (1949) table showing the number of green leaves per shoot from the spring of 1939, when growth began, until the spring of 1940, when an inflorescence was produced, is presented below:

TABLE IX
AVERAGE NUMBER OF GREEN LEAVES PER SHOOT IN NON-FERTILIZED PLOTS,
ON 7 SHOOTS, EACH OF WHICH HAD A TOTAL OF EITHER 17 OR 18 LEAVES

Year	Month	Average number of green leaves		
		Entirely green	Partially green	Total
1939	May 18	2.0	.6	2.6
	June 2	1.9	.7	2.6
	June 17	1.3	1.4	2.7
	July 2	1.7	1.9	3.6
	July 17	2.0	2.0	4.0
	August 1	1.9	2.6	4.5
	August 16	2.0	2.7	4.7
	September 3	1.7	2.1	3.8
	September 18	2.0	2.3	4.3
	October 1	1.6	2.3	3.9
	October 18	1.9	2.0	3.9
	November 7-14	1.7	1.9	3.6
1940	April 1-2	1.1	1.6	2.7
	April 15-16	2.1	1.6	3.7
	May 4	3.0	1.1	4.1
	May 17	2.6	1.4	4.0
	June 3	1.3	.9	2.2
	June 17	0	.3	.3

Midsummer Depression.—Shortage of water is probably partly responsible for periods of slow growth of leaves during midsummer. Brown (1943) has shown that irrigation during periods of drought or low soil moisture helped considerably to increase yields. Ahlgren (1938) stated that moisture, more than any other factor, limited forage production. While summer irrigation may maintain yields, summer growth is made at the expense of stored reserves and may reduce the competitive ability of bluegrass against weeds (Brown, 1943). Irrigation during midsummer is probably less important than during a dry fall. Brown found fall droughts to have a decided adverse effect on bluegrass yields. Irrigation during fall and early winter is not commonly practiced, but the indications are that it would encourage root growth and tillering and thus greatly aid the grass in its competition with annual weeds.

Numerous studies have shown that peak yields of forage occur twice during the year, usually in late spring and in late August or early September (Brown, 1943). Examination of series of leaves produced by various individual plants

show that usually the midsummer leaf is slightly shorter than those immediately preceding or following it (text-fig. 29). This may be connected with the period of maximum summer temperatures which commonly occur in July. Both Harrison (1934) and Darrow (1939) have shown shortness of leaf to result at temperatures ranging between 95 and 100° F.

Since irrigation did not completely eliminate a midsummer depression of yield, Brown (1939) attributed part of the reduction to supra-optimal temperatures. Whether these midsummer depressions of forage and of leaf length are interrelated cannot be said. The spring peak can easily be understood as being a combination of factors including inflorescence development, high available nitrogen, and plenty of water, but the late August peak is more difficult to explain, unless we merely assume it indicates a return of more nearly optimum conditions.

BUDS ON THE CROWN

The Number of Buds Produced.—In a given habitat individual bluegrass plants will produce new leaves at almost the same rate, and at the end of the year will all have about the same number of leaves (table VII). In a meadow this number averages about 12–14; in a very dry shady locality, 7–9; while in a well-watered pasture it may well be as high as 18. Since under ordinary growing conditions only a single leaf blade grows at once, the longer the leaf the fewer will be the number of leaves in a given season. This accounts in part for the low number of leaves in dry shady places, for there the leaves are very long and growth is slow. In grazed places, leaves are short and the soil usually well fertilized so that growth is rapid. Consequently more leaves than normal appear. Such factors as this play an important role in the ultimate appearance and behaviour of a plant.

The number of leaves reflects the number of phytomers formed during a given period and consequently the number of buds available for rhizomes and tillers. It is very uncommon to find that all the buds on a crown have matured into new shoots, for the buds of midsummer phytomers frequently remain dormant indefinitely, thus limiting branching to the fall and winter and early spring buds. This is especially true in the case of old meadow plants.

A Conservative Crown.—Instead of speaking in abstract terms, it would be well to examine some actual plants. Text-figure 30 shows a diagram of an extremely conservative three-year-old specimen from an old meadow in early November of 1948. A photograph of the basal part of a very similar plant is shown in pl. 9, fig. 30, although only a single year's growth is included. It can be seen that in both plants only the bare minimum of buds have developed into new shoots. In text-fig. 30 two generations of inflorescences are shown, one for 1948 (I 48) and one for 1947 (I 47). On the basis of these facts, it is simple enough to put together the history of this plant. It had its beginning probably as an intravaginal shoot from some plant now long since dead. That was in the fall of 1945. During the summer of 1946 no buds developed into rhizomes, but in the fall three intravaginal shoots developed from the last three buds of the year, the 14th, 15th, and

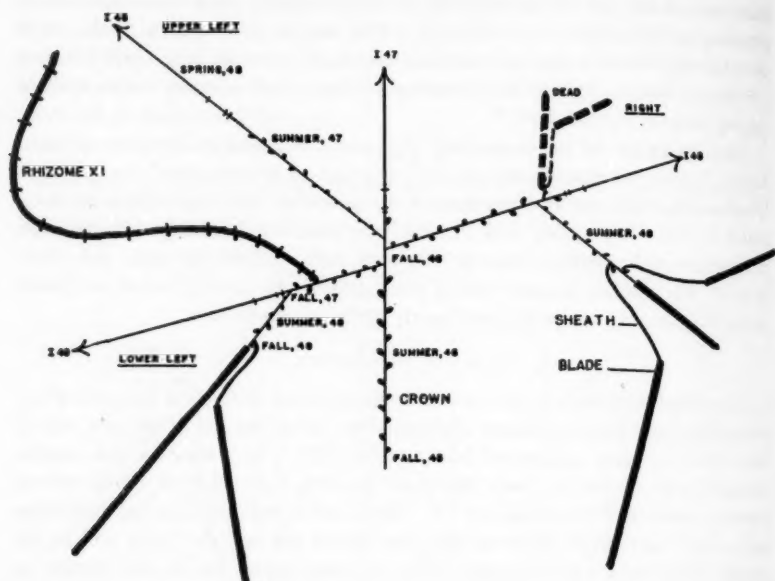


Fig. 30. Diagram of a conservative old meadow bluegrass plant. Very little branching has occurred during its three years of growth. There are few tillers, few rhizomes and most of the growing points have terminated in inflorescences. Sheath and blade, $\times \frac{1}{4}$; crown, $\times \frac{1}{2}$.

16th. Buds 17 and 18 which developed after the intravaginal shooting occurred should properly be considered part of the following year's growth. This main stem ended its terminal growth by developing into an inflorescence in the summer of 1947.

If we now follow the destiny of its three shoots we find that each of them pursued a somewhat similar course, at least to the extent that in 1948 they all terminated in a flowering shoot. There were, however, some interesting differences. The last shoot (text-fig. 30, upper left) did not produce any branches from its 13 buds in 1947 and thus died. The next to last shoot (right) produced 13 buds also, the last two of which developed into tillers in the fall of 1947. One of these shoots died at an early stage. In the meantime the first original shoot (lower left) produced only 10 buds of which one developed into an intravaginal shoot in the fall of 1947, and another produced a rhizome in the following summer. It will be noticed that this 1948 rhizome developed from a bud just a little below the tiller of the fall of 1947; this is the usual place of origin of most summer rhizomes when only a few develop. This rhizome is easily identified as having been produced in summer because of its length and large number of internodes.

If we follow the history of this plant into the third (1948) generation, we find that there are only three living descendants, two shoots and a rhizome. The surviving tiller on the right had produced 10 buds in 1948 up to the time it was dug up. The tiller on the left side produced only 6 buds. If we assume that only one more bud would have been added during the remainder of 1948, then the following numbers of buds were produced in each of the three years on the respective shoots:

	Upper left	Right	Lower left
Main shoot, 1946	16		
Tillers, 1947	13	13	10
Tillers, 1948	(died)	11	7

These data strongly suggest that the longer a plant lives by intravaginal shooting only, the fewer leaves are produced each year. It is also striking that over a period of three years one growing point has only increased to three new growing points, of which one is a rhizome, and two are relatively unproductive tillers.

The existence of such a conservative plant is a very precarious one. It represents the bluegrass plant at its minimum, with 1 rhizome, 4 inflorescences, and 6 intravaginal shoots being produced in a little less than three years out of a total of 74 buds.

A Vigorous Specimen.—In decided contrast to this old meadow bluegrass plant is the closely grazed pasture plant shown in text-fig. 31, which was also dug up in early November, 1948. Here the basic seasonal pattern is all but obscured. The main stem of 16 buds is much exaggerated in the drawing so that all the branching could be included. This stem developed during the year of 1947. In the fall of that year it gave rise to six branches, of which two have been broken off. Of the remaining four, the lower two, arising from buds 8 and 10, became short rhizomes, and the upper two, from buds 15 and 16, are intravaginal shoots. This main stem terminated its growth by flowering in 1948. During the spring and summer of 1948, when livestock were put on the pasture, considerable late-summer rhizome development resulted (branches A-H) and some fall rhizomes are present (I-K). The two can be distinguished because fall tillers have appeared only on the summer rhizomes; also the fall rhizomes have only one or two leaves. L and M are intermediate types. When the plant was dug up it was busy producing tillers in the axils of new fall leaves. Some branches show as many as four such tillers, and in branch F some of the tillers have already produced secondary shoots. Figure 31 (pl. 9) is a photograph of a crown region from a plant which was similar in all respects to the one shown in text-fig. 31. It bears an especially close similarity to the shoot just to the left of the 1948 inflorescence.

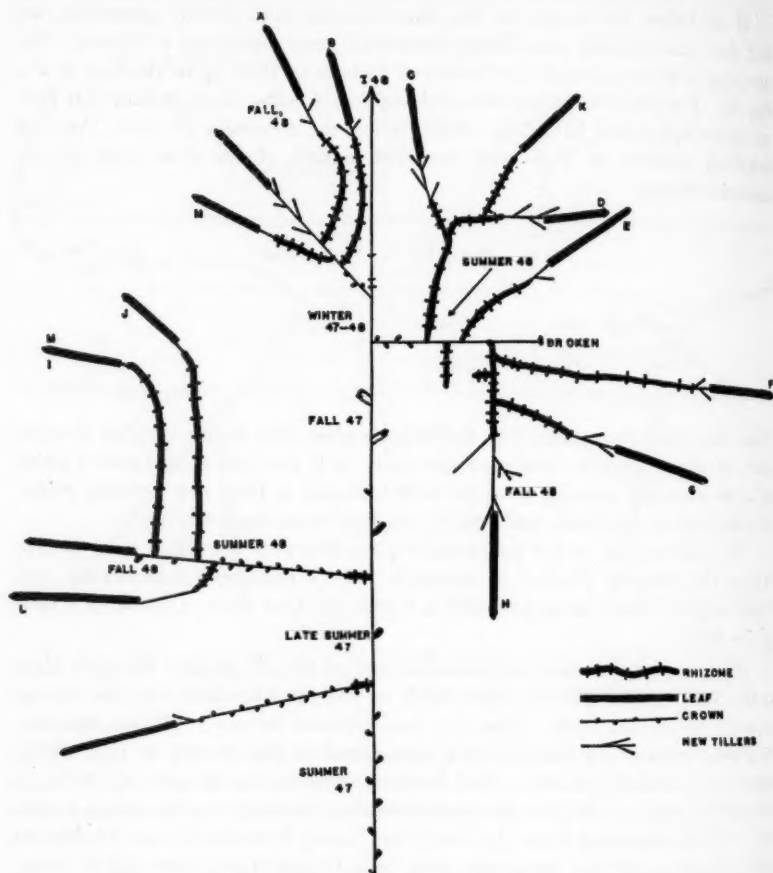


Fig. 31. Diagram of a vigorous pasture plant. Considerable development of both tillers and rhizomes has taken place during a year and a half of growth. Rhizome, $\times \frac{1}{5}$; leaf, $\times \frac{1}{4}$; crown, $\times \frac{1}{3}$.

To recapitulate, from a single plant in 1947, six shoots developed, two of which were broken off. Summer and fall rhizoming in 1948 increased the number of growing points by 13, and intravaginal shooting added 28 more to make a total of 45 active growing points out of a total of 138 buds. The net results of less than two years growth were: 15 rhizomes, 30 shoots and 1 inflorescence.

A Hypothetical Individual.—After examining these typical plants we may be a little closer to discerning the basic bluegrass theme together with its variations. Perhaps we can now draw a hypothetical average plant if we limit ourselves to generalities. Let us begin with a rhizome which appears at the surface of the soil

sometime in late winter or early spring as rhizomes frequently do (text-fig. 32 A-D). Such a plant will not develop any tillers. Instead, its winter and early spring buds will lie dormant while rapid leaf growth takes place. About mid-April these buds will start to swell and develop into new rhizomes. The first new rhizome will probably be short; the next ones longer; and some may grow underground for several summer months. Most of the winter and spring buds will be thus consumed in the production of rhizomes, while the late spring and early summer buds of the parent plant are gradually suppressed so that no new branching takes place. The suppression of these buds is probably related to the cessation of root initiation which Sprague (1933) has shown to take place early in May. Nishimura (1923) has indicated that no vegetative bud elongates until a root is produced. If this is true, summer dormancy is inevitable.

The sprout-like rhizomes previously mentioned as appearing in late August under rank meadow conditions would be most apt to occur on old crowns, especially on those which bloomed in spring. Rhizomes of the year, such as the one we are describing, would not commonly show them.

The change which comes over bluegrass in early fall brings with it shorter, greener leaves and white, short roots. The late summer buds, instead of remaining small, discolored and dormant, become increasingly white and well developed, but they do not usually produce rhizomes immediately. Instead, they are transitional in nature and anticipate the appearance of tillers from fall buds (pl. 9, fig. 32). Short fall rhizomes may, however, appear after several tillers have begun to function efficiently. Frequently no rhizoming at all takes place in the autumn, and the buds are thus conserved for a rapid development of rhizomes the following spring about the time the inflorescences begin to appear.

There is a conflict between rhizome and shoots for the buds of fall. Since the intravaginal shoot arises almost as soon as the bud is formed it has first choice. If conditions are right, practically all fall buds may become tillers, and thus only one or two buds will remain on the main stem from which rhizomes may appear the following spring. Where only the latest fall buds develop into tillers there is room for three or four rhizomes preceding them. If we pull these plants from the soil in late May, the former will be found to have many short leaves, and, at the most, one rhizome, and the latter will have a few long leaves and quite a few rhizomes. All rhizomes, however, do not turn up in early spring as did our hypothetical one. Some turn up throughout the summer, others in the fall. A rhizome turned up in fall is shown in text-fig. 33 A-C, for the sake of contrast. This plant begins life by tillering instead of rhizoming. Every bud at first is taken up by tillers, with the frequent exception of the lowest bud on the crown which usually remains available for production of a rhizome in the spring. In a pasture grazed closely the previous fall there are many plants of this type to be found the following spring.

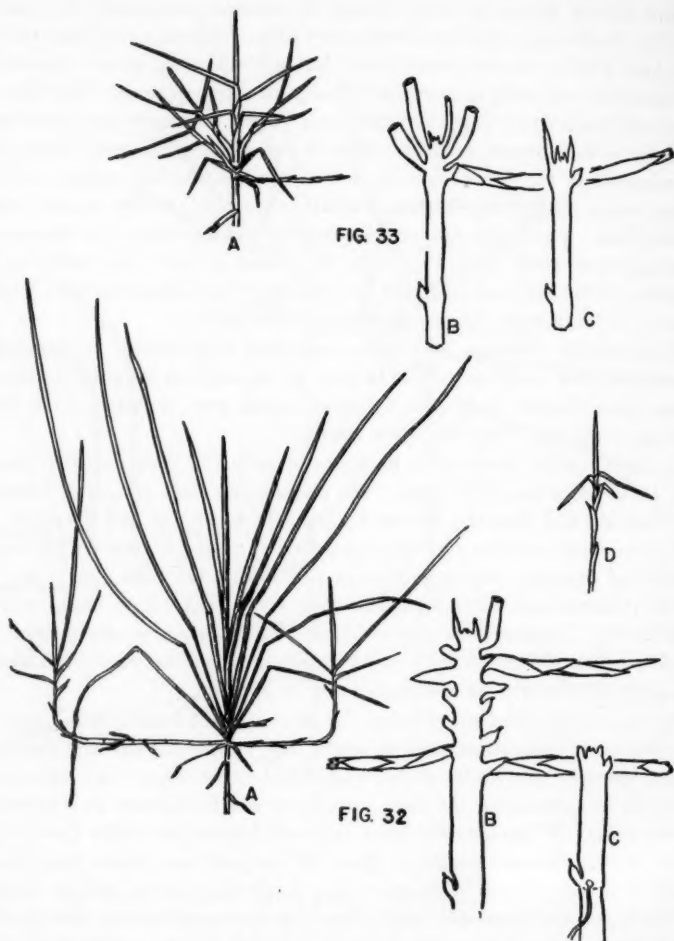


Fig. 32. A, a rhizome turning up in the spring will look like this in the fall. Summer rhizomes have turned up and formed new plants. A single short fall rhizome is developing, $\times \frac{1}{2}$. B, the crown of this same plant, showing upper buds developing into tillers, $\times 2\frac{1}{2}$. C, the crown in the spring just after having turned up, $\times 2\frac{1}{2}$. D, above, the turned-up rhizome.

Fig. 33. A, a spring plant derived from a fall rhizome, with three tillers and short winter leaves, $\times \frac{1}{2}$. B, the crown in spring, with only a single rhizome at the base, the remaining buds occupied by tillers, $\times 2$. C, the crown in fall shortly after having turned up, $\times 2$.

Some Practical Considerations.—While the seasonal effect is more or less the same, the record of events as recorded by various generations of rhizomes will be slightly different. The proportion of rhizomes of a given vintage in a sod or a nursery plot may change considerably depending on the age of the stand, the treatment it receives, or on the weather. Evans and Ely (1935) have presented figures which show the extent of such variation within two successive years:

TABLE X
AVERAGE NUMBER OF NEW RHIZOMES PER PLANT IN DIFFERENT MONTHS IN 1932
AND 1933 ON PLANTS TRANSPLANTED ON MAY 18, 1931, TO CULTIVATED
ROW PLATS. (THE PLANTS WERE NOT CLIPPED AT ALL.)

Month	1932	1933
April		0.0
May		0.3
June	15.5	5.3
July	18.3	2.0
August	3.3	21.0
September	0.3	6.0
October	2.3	0.5
November	3.0	

Wherever studies of bluegrass are made, the sequence of events and their possible variation must be kept in mind. Undoubtedly, elaborate quantitative tests of rhizome production, top production, or other aspects of the plants' growth have failed to obtain consistent or statistically significant results because of the failure to reckon with the flexible nature of the species. In pot experiments with nutrient solution it is doubly important to know the kind of material being grown in the pots. Such factors as the number of buds available on a transplanted rhizome or crown, the time of year such buds developed, the length of the associated leaf, and whether the rhizome is from a turf or a nursery row will all have repercussions on the results.

DESIGNING A BLUEGRASS PLANT

THE SPECIFICATIONS

How we manage bluegrass will depend on how we intend to use it. Bluegrass is called upon to serve many purposes, including the following:

Pasture	Range	Meadow	Conservation	Turf
Alternating	Winter	Hay	Sod run-off strips	Lawns
Continuous	Summer	Silage	Terrace plantings	Greens
Dairy	Breeding		Roadsides	Fairways
Fattening				Playing fields
Subsistence				Landing fields

With adequate study of each environment and of the factors involved in each type of use, a blueprint could be drawn showing the specifications of the plant needed. There would always be some conflicts. It might be a simple matter to

design a plant for yield in one year, but consideration would have to be given the repercussions of management techniques on future production. There is a strong likelihood that the most efficient treatment of a bluegrass stand might involve making different use of it in successive years. Under some conditions this is not feasible so a compromise must be made.

THE MATERIALS AND THE LABOR

We have found that the bluegrass plant is a flexible collection of buds whose destiny, while in part controlled by inaccessible aspects of its environment, can also be molded by specific practices. Once the requirements are known, we can choose from the following alternatives:

1. *Many vs. Few Buds.*—The highest production of buds comes with short leaves, moist, nitrogen-rich soil, and sunny conditions. Where intensive management is necessary, usually the more buds the better. If long leaves are desirable then some sacrifice of buds is inevitable.

2. *Dormant vs. Sprouted Buds.*—Greatest sprouting of buds occurs in good soil with plenty of aeration and little competition, and seems to be aided by high organic-matter content and adequate water supply. (It is just such requirements which Percival (1921) specifies as necessary for maximum development of tillers in the wheat plant.) It is generally desirable to have a large proportion of the buds on a plant develop. This can be carried to extremes, however, as discussed in the next section. If the need is for a tight sod, then competition among individuals will necessarily follow, and some loss of sprouting ability will be encountered.

3. *Rhizomes vs. Tillers.*—Tiller production is encouraged by provision of good soil conditions as described above. Treatments which specifically favor tillers include fall grazing or mowing, fall nitrogen fertilization, removal of all shading growth and dead weeds, and in dry falls the addition of moisture. Maximum tillering may not always be desirable. It can result in what one might call an excessive investment in growing points, considering the amount of capital (soil, oxygen, water, and nutrients) which the plant has within reach. Ideal conditions are necessary to support large numbers of closely packed shoots even though they are capable of forming their own adventitious roots. When such plants are subjected to excessive mowing or grazing or treading their reserves can be very rapidly depleted. This is especially true since strongly tillering plants seldom have very extensive underground parts. In general, it should be stressed that if shooting is to be encouraged in fall, then adequate provision should be made to provide optimum conditions for growth in the following spring, especially through nitrogen and potassium fertilization.

Rhizome development depends in part on how extensive the fall tillering process has been. If most of the fall and winter buds have been used up, rhizomes are apt to be uncommon. The same ideal soil conditions which encourage sprouting of other buds favor the production of rhizomes. Plants which grow in open soil

as spaced seedlings or shoots in nursery plots are abnormally productive. Balanced fertilization in winter, spring, or summer favors increased rhizoming. Phillippe (1943) found that in nutrient culture, maximum rhizome production occurred under conditions of moderate nitrogen concentration (17 to 57 PPM) and by fairly high potassium concentrations (41 to 162 PPM). High nitrogen content has been found by numerous investigators to reduce rhizome production in pot and nutrient experiments. Brown (1943) has stated that summer irrigation leads to the death of many summer rhizomes, and Harrison (1934) found combinations of close clipping and temperatures around 100° F. to be fatal. This coincides with observations of Wilkins (1935) that over-grazing during drought periods when temperatures were around 100° F. reduced bluegrass recovery the following fall by 75-99 per cent.

To some extent rhizome production is self-regulatory. Usually whenever high production is a possibility, as in new seedlings or broken sods, some benefit may be derived from much rhizome growth. When sods are tight, then fewer buds sprout. Under an old sod, rhizome production apparently reaches an approximate equilibrium with the available soil nutrients, especially nitrogen. There is adequate decomposition of a certain amount of dead rhizome matter plus just sufficiently vigorous growth of the plant itself, so that no more rhizomes will be added to the soil that can be broken down the following year. Some fluctuations in this cycle will occur with weather variations.

A certain amount of rhizome production is essential under most conditions because intravaginal shoots seldom persist for more than a year. It is also important, in view of the many advantages of rhizome herbage production, such as the broader, more vigorous leaves, more even distribution of roots, growing point well below the soil, shorter sheaths, and leaves close to the soil, that plants are not completely defoliated by grazing. There is little doubt, however, that too high a proportion of rhizomes in the stand may lead to low herbage productivity, for they respire and consume soil oxygen, and sooner or later die, and the micro-organisms which break them down compete with the grass itself for soil nutrients. This is especially true since rhizomes are high in carbohydrates and low in nitrogen.

It is commonly found that where fields or plats are mowed during the summer for a period of years, total forage production falls off. Ahlgren (1938) states: "The data show that with the exception of 1933 (the second year) there was a progressive and significant decrease in the yield of bluegrass on all plats, regardless of the cutting or fertilizer treatment used during the period 1932-1936 inclusive." His data follow:

Year	4-inch cut		Hay cut	
	No fertilizer	Fertilizer	No fertilizer	Fertilizer
1932	1,619	3,113	2,050	3,957
1933	2,153	4,295	2,977	4,579
1934	1,817	2,114	1,681	2,046
1935	1,520	1,932	1,279	1,785
1936	826	1,703	435	1,617

(This test was begun on old sod. The first cuts were made as above, to a level of $1\frac{1}{2}$ ". Subsequent cuts were made to $1\frac{1}{2}$ " level when the grass reached a height of 4-5". Figures are pounds per acre.)

The cause of this progressive decrease in production has not been adequately explained, but there is a strong possibility that the accumulation of rhizomes in the soil may be involved. That such accumulations occur are well shown by data from Brown (1943):

Year	Herbage yields			Root Yields			Rhizome Yields		
	1"	2½"	Hay	1"	2½"	Hay	1"	2½"	Hay
1937	2833	2254	5857	1927	2049	1922	122	122	108
1938	508	310	1280	1897	2137	2210	372	478	505
1939	382	141	501	1979	2289	2281	398	519	507
1940†	1286	900	1601	1946	2088	2455	660	817	1071

† NaNO_3 added 100 lbs. per acre March 15 and semi-monthly at rate of 50 lbs. per acre from April to June 15 and from Aug. 15 to Sept. 30. These test plots were seeded in Sept., 1936. Figures are lbs./acre. $1\frac{1}{2}$ "- and $2\frac{1}{2}$ "-inch cuts were made semi-monthly. Hay cuts made at full bloom and at end of growing season.

The same progressive decrease in yields of herbage are apparent here. In both of these experiments, the removal of clippings from the plots probably exerted some influence on total yields. It is clear, however, that reduction in yield paralleled an accumulation of rhizomes. Brown has stated that death of rhizomes began in the second year, and in the fall of the third year there were so many dead ones that they were separated from the live ones and not included in the data. Therefore the figures above do not show the total accumulation of rhizome material in the soil. The data would have been even more striking had all dead material been included.

Typically, maximum herbage yields were secured the first year after seeding. In that year the rhizome dry matter in the soil was less than 5 per cent of the total dry weight of the herbage and rhizomes together. By the third year herbage yields had dropped from eight to sixteen times, but rhizome weight had increased from three to five times. Rhizomes had come to make up 50 per cent or more of the total

dry weight exclusive of roots (which had a remarkably constant dry weight throughout the tests). Significantly, the least amount of rhizome dry weight was produced when the grass was mowed semi-monthly to a 1-inch level. Most of this difference probably involved rhizome length rather than number.

In the fourth year heavy nitrogen fertilization in spring and summer increased herbage yields from three to six times but at the same time the rhizome dry matter was nearly doubled. Addition of nitrogen in both Ahlgren's and Brown's tests increased yields but did not completely restore productivity to its former level. According to the data above, rhizome production was greatly increased by fertilization in spring and summer, and the sod-bound condition could be expected to become worse the following year.

Moderate mowing of pastures in early spring through summer apparently will increase the rhizomes in the soil in proportion to the amount of tops above ground, even when mowing may be semi-weekly to a height of 1 inch. Increase of rhizomes goes on until the stand is almost devoid of herbage value. Rhizomes do eventually turn up and add to the herbage total, but there is considerable delay and wasted energy in getting top production through rhizomatous plants alone. Not only that, but at the most an ordinary plant cannot be expected to bear more than four or five rhizomes while its potential of new tillers is considerably greater when properly managed.

The 2½-inch height such as that advised for most lawn mowing resulted, in Brown's experiments, in the highest proportion of rhizomes to tops. This would give a tough sod, but relatively little top growth, unless some counteracting practice designed to stimulate intravaginal shooting and long leaf growth were used.

Kentucky bluegrass is really a plant with a split personality. It is trying to be rhizomatous, as is its relative, Canada bluegrass, and upright, as is *Poa trivialis*. It actually can assume either role, and it is up to the pasture or turf manager to decide which personality or complex he prefers.

It is not surprising that to some extent bluegrass has lost some ground in the field of intensive pasturing to non-rhizomatous grasses and legumes, for these species do not waste energy and nitrogen on non-leafy production. Admittedly, bluegrass cannot compete with such productive non-rhizomatous types as alfalfa, perennial ryegrass, orchard grass, and ladino clover, but its quick adaptability and persistent nature are indispensable attributes under many conditions. To make maximum use of the species, however, close attention must be paid to its seasonal rhythm and its system of bud economy.

4. *Long vs. Short Rhizomes.*—Summer rhizomes are long, and fall rhizomes are short, but close and continuous grazing leads to short rhizomes at any time. In pot cultures Harrison (1934) found that high nitrogen content encourages short rhizomes. Length of internode has little or no relation to ultimate length of the rhizome. Dry periods shorten internodes but variation in nutrient balances has been shown by Phillippe (1943) to have no significant effect.

Short rhizomes are desirable in some cases, long ones in others. If a tight sod is required, rhizomes of moderate length must be encouraged. Stands which have only short and shallow rhizomes will have little protection under very hot and dry conditions. If properly managed, however, short as opposed to long rhizomes could be counted on to increase the efficiency of a pasture or lawn.

5. *Branched vs. Unbranched Rhizomes.*—Branching of rhizomes is encouraged by those conditions which favor the development and sprouting of buds. Damage to the initial growing point stimulates axillary buds to develop, and wherever summer sods are burned or mistreated, or submerged by dense weed growth or by alluvium, the ability of rhizomes to sprout in early fall from their axillary buds is of great importance to the survival of the plant. The vigor of the rhizome determines how many buds develop, and whether they will form strong rhizome-like branches or merely delicate vertical shoots. For those strains of grass which are primarily rhizomatous, thickness of the stand is almost completely dependent on the ability of the rhizome to produce branches.

6. *Vegetative vs. Reproductive Shoots.*—The number of reproductive shoots produced in May depends on two things, the number of plants which are adequately mature and vigorous enough to undergo flower initiation in the previous fall, and the number of tillers which these plants produce. Plants which are mature and vigorous in fall will have come largely from rhizomes turned up during the previous fall, spring, and early summer. Some perennial tillers will contribute to the cause. Ultimately then, to influence the potential seed crop it is necessary to start work a year and a half ahead of harvest time. Encouragement of rhizomes, followed by encouragement of tillering, followed by encouragement of long leaves and full panicles as described below, should give maximum seed yields. This would leave the soil full of old rhizomes, and unless steps were promptly taken to deplete their reserve carbohydrates through grazing and encouragement of tillering the following fall, subsequent yields would suffer. A complete management plan would be more complex than this, but these are the main considerations. Such a plan might also provide high yields of hay or silage, but maximum development of inflorescence may not always be desirable. Limitation of flowering can be accomplished through heavy grazing in late summer and fall, and by grazing or mowing in spring when the panicles are exerting. Encouragement of a vegetative condition in bluegrass holds back the spring flush of growth which accompanies the development of the flowering shoot. It also holds the protein content of the grass at a fairly high level, while the carbohydrates are kept low (Woodman et al., 1928; Hein, 1937). This would limit the gaining of weight by fattening animals in preparation for fall markets or over-wintering. It would, on the other hand, encourage summer milk production in a dairy or breeding herd.

7. *Short and Wide vs. Long and Narrow Leaves.*—Short, wide leaves and excessive tillering often go together. Long leaves are encouraged by winter and spring fertilization. When heavily tillered plants are fertilized in winter and spring a very

dense, moderately long and wide-leaved blue-green plant is produced which is highly productive. It combines the advantages of the other types.

Constant grazing or mowing keeps grass leaves short, probably for two main reasons. First, without the over-burden of shading tops, the blades reach the light rapidly and do not become attenuated. Second, such treatment encourages the production of many short rhizomes the early leaves of which are commonly somewhat abbreviated. Infrequent mowing or grazing has little effect on leaf length. While long-leaved plants are commonly considered more productive of herbage, the fact remains that short, wide-leaved foliage is more palatable to livestock. They will barely consider the rank growth of mid-summer meadows.

8. *Heavy Seed Production vs. Little Seed.*—There is a complex relationship between number of panicles and number of seed produced. In general, number of panicles is increased by mowing or high nitrogen fertilization in fall (Spencer et al., 1949; Nillson-Leissner, 1937). This treatment, however, usually reduces the panicle length and the culm length and reduces the number of seed set per panicle when compared to spring fertilization (Phillippe, 1943; Spencer et al., 1949; Nillson-Leissner, 1937). Winter or very early spring fertilization tends to give tall panicles and inflorescences, but does not increase the number significantly. Seed production is generally good. Late spring applications in April, when the panicle is growing, tends to encourage leaf growth rather than inflorescence development, and results in a weakening of the culm and reduction in quality of the seed.

9. *Sod vs. Open Growth.*—Bluegrass, like most other plants, grows most profusely when grown alone. When it is allowed to sod over, then we inevitably lose production, whether it be of forage or seed. In this respect it is significant that bluegrass plants growing in alluvium produce by far the greatest amount of seed per panicle, bear a goodly number of panicles, have large seeds, and long and wide leaves. A year-round supply of water, rich soil, and sun combine to produce maximum yields. Inevitably in a sod we have to sacrifice some greenness, some vigor, some thickness of stand. From a productivity standpoint the best that can be done is to provide management practices which make the sod-grass think it is down by the river. Discing and harrowing aid in this simulation by providing loosened and bare soil areas. To avoid weediness treatment should be done only in fairly late fall when tillering, rooting, and fall rhizoming together can recover the vacant areas while weed growth is at a minimum. Another way of getting the productivity of the river bottom up on the pasture is by using alluvial ecotypes for seed. This process is going on more or less unconsciously in many grass-breeding experiments. So-called high-producing strains of many species invariably bear a striking resemblance to river-bottom types.

THE PARTS OF THE BLUEGRASS PLANT COMPARED⁵

WHERE DO THEY ORIGINATE?

Rhizome.—From underground, axillary, mature buds whose subtending leaves are dead, or dying. April–May extension type predominantly from buds of early fall and early spring. August sprout type from spring and summer buds, and fall rhizomes from early fall buds.

Crown.—From underground terminal buds of rhizomes, seedlings, or intravaginal shoots. May sometimes be above ground, especially in seedlings and shaded shoots.

Tiller.—From axillary buds below or above ground on late fall and early winter phytomers.

Culm.—From terminal bud of crowns of sufficient maturity. If from a rhizome, the crown will not have less than 6–8 leaves; if a tiller may have only 2.

Panicle.—Main axis or rachis is continuation of culm. Side branches arise as secondary, tertiary, and quaternary protuberances from this rachis.

Spikelet.—Some time in April.

WHEN DO THEY BEGIN TO FORM?

Rhizome.—Principally early May, concomitant with flowering, but to some extent throughout early summer; also in fall, early or late, depending on condition of grass. Sprout type in late August or early September on rank meadow type or burned or damaged areas. In closely grazed places on good soil almost all year except late winter.

Crown.—When rhizome turns up, especially late summer and early fall, and late fall and early spring. From tillers in late fall and winter and from seedlings in fall and spring.

Tiller.—Early fall to late winter, principally late fall.

Culm.—Internodes develop in late fall and winter following initiation of intravaginal shoots.

Panicle.—Winter and early spring; may not form until early March (Musgrave, 1940).

Spikelet.—Some time in April.

NUMBER ON A PLANT OF 16 PHYTOMERS PER YEAR

Rhizome.—Varies greatly, 0–8, average probably 2, but including secondary and tertiary plants may be 4–6.

Crown.—Main crown, plus average number of turned-up rhizomes (2) plus average number of tillers (3, see below) gives average of 6; may be greatly amplified by secondary and tertiary budding.

Tiller.—Average around 3, less than 1 or more than 10 infrequent; with secondary branching may reach 50.

Culm.—Usually 1 on main axis and 1 on each of 1 or 2 tillers. May be up to 12 per plant with multiple tillering.

Panicle.—One per culm; number of protuberances may vary greatly; average 3–5 at each node of rachis. There are from 5–10 rachis nodes, therefore 15–40 branches on main axis. Secondary and tertiary tillers have fewer.

Spikelet.—Average number not counted. Secondary and tertiary tillers have fewer.

TO WHAT EXTENT DO THE PARTS BRANCH?

Rhizome.—Usually limited; can be extensive.

Crown.—Branching includes rhizomes or tillers. Of 16 buds, not more than half usually develop.

Tiller.—Branches as does crown; may form rhizomes or secondary tillers, but only the latter in first fall and winter. Rhizomes rarely appear until following May, from any left-over buds.

Culm.—Does not branch (no buds present).

Panicle.—Almost all buds develop.

Spikelet.—Basal phytomers including the two glumes and lowest lemma do not usually bear branches. Upper phytomers bear florets.

⁵ These data are a composite of information from authors previously credited, and from observations made in the course of the present study. They are in most cases very approximate, and variation could not always be taken into consideration due to lack of data. Most of the data pertain to bluegrass growing in Missouri.

THE LENGTH OF THE INTERNODES

Rhizome.—Highly variable in length, 1–50 mm., average 10–15. Shorter in dry soils or dry periods.

Crown.—Minute, somewhat less than 1 mm.; individual internodes can be induced to elongate by shading or covering plant with soil.

Tiller.—Same as for crown.

Culm.—Gradational, the first a few mm., the last up to 30 cm. or more. Successive internodes plotted on a logarithmic scale fall on a straight line, under normal conditions. (See Prat, 1934.)

Panicle.—Gradational on rachis, in reverse order to internodes of culm. Range from 30 to 2 mm., but do not form a straight line on either natural or logarithmic scale.

Spikelet.—Longest below first glume, 1–3 mm.; rest are minute.

THE NUMBER OF INTERNODES

Rhizome.—Many in summer extensor rhizomes—may be up to 30. Fall rhizomes seldom show as many as 10, usually 5 or 6.

Crown.—Depends on habitat and season. From 7 to 18 a year.

Tiller.—Same as for crown, but few tillers persist for a whole year. If they do, there tend to be fewer phytomers each year.

Culm.—3–5, usually 4, rarely 6.

Panicle.—Rachis 5–10, main branches about the same, branches of lower order successively fewer.

Spikelet.—Averages 6, varies from 4–10 (includes 3 sterile and 3 or more fertile).

HOW FAST DO ITS INTERNODES ELONGATE?

Rhizome.—2–5 mm. per day.

Crown.—No elongation.

Tiller.—No elongation.

Culm.—Varies with the internode number. Internode 1, 0.5 mm. per day; Internode 2 and 3, 4 mm. per day; Internode 4, 7.5 mm. per day.

Panicle.—7 mm. per day for rachis as a whole.

Spikelet.—Very little if any elongation.

THE SHAPE OF THE INTERNODE; IS IT SOLID OR HOLLOW?

Rhizome.—Compressed dorsoventrally, solid.

Crown.—Round, solid.

Tiller.—Round, solid.

Culm.—Round, hollow.

Penicle.—Round, somewhat ribbed and grooved at extremities; hollow, solid at extremities.

Spikelet.—Not examined.

WHAT KIND OF LEAVES, IF ANY, DOES IT BEAR?

Rhizome.—Cataphylls only; very short blades may appear (up to 2 or 3 mm.) without turning up.

Crown.—First leaves with fairly short blade, shorter than sheath; later, blade is longer.

Tiller.—Leaves as for crown, but first leaf is enclosed in prophyll.

Culm.—Normal leaf at base, upper leaf has very short blade and long sheath. Others transitional. No leaf on last internode.

Panicle.—No leaves.

Spikelet.—Presumably glumes are sheath part of leaf; palea is prophyll of the shoot which becomes the floret.

WHAT POSITION DOES EACH PART ASSUME?

Rhizome.—Horizontal, inverted arch, almost upright, or may show some geotropism at first.

Crown.—Horizontal to vertical.

Tiller.—Nearly prostrate to erect.

Culm.—Usually vertical, though under special conditions may be prostrate or procumbent.

Panicle.—Attitude of rachis same as culm. Branches may be appressed to drooping, though usually at right angles.

Spikelet.—Florets usually fairly closely appressed.

WHAT IS THE NORMAL LIFE OF EACH PART?

Rhizome.—May turn up within a few days after it begins to grow, or may stay underground 60 days or more in summer. During cold weather remains underground while soil is frozen.

Crown.—Matures with development of flowering shoot; shortest period is on fall intravaginal shoots, only 6-7 months. Rhizomes which turn up in late summer may bloom in 9 or 10 months, and intravaginal shoots which do not bloom first year may bloom in 1 year and 6 months. Fall seedlings take 1 year and 8 months and spring seedlings 1 year and 3 months.

Tiller.—6 months, or 1 year and 6 months.

Culm.—Initiation of the phytomers involved takes only a short time in late fall; elongation in spring takes about 1 month. Total life is about 6 months.

Panicle.—5 months for elaboration of branching system, 9 or 10 days for elongation of the panicle proper, and 45 days for its complete exertion including culm elongation.

Spikelet.—First spikelet starts to form when panicle is about $\frac{1}{4}$ inch long. At 1 inch there are at least 3 rudimentary florets. Glumes enclose entire spikelet at $1\frac{1}{2}$ inches (Musgrave, 1940). This would be 5-7 days. Total maturity time, to exertion of anthers, about 5-6 weeks.

HOW FAST ARE NEW PHYTOMERS INITIATED?

Rhizome.—Rapidly, averaging nearly one every two days during summer.

Crown.—Average around 13-14 a year, exclusive of inflorescence. Slow in winter and hot or dry periods of summer; rapid in spring and for a brief period in early fall. A new leaf every 15-20 days in spring and early fall; every 30 to 50 days in summer and late fall; and every 60 days or more in winter.

Tiller.—Same as for crown.

Culm.—4 phytomers of the culm produced some time in late fall but rate not known.

Panicle.—Assuming 8 internodes on each rachis in period January 1 to April 1, rate is about 1 phytomer every 11 days. Comparable rate on vegetative part is 1 about every 60 days. Rate of branching is different, depending on strain and time of year; averages about one new generation every 40 days according to data in Evans (1949).

Spikelet.—A spikelet with 3 rudimentary florets develops in about 6 days (Musgrave, 1940); including glumes this is about 1 phytomer per day.

THE FREEDOM OF THE PHYTOMER

A grass plant is a community of phytomers. No phytomer exists autonomously, but is necessarily involved in the total effort of the plant. At the same time, in its extreme youth an individual phytomer is quite plastic and may, as it ages, develop into any one of a number of things. It may or may not take full advantage of its potentialities to produce leaf blade and sheath, internode, root, and bud. It may consist only of an internode, as in the case of the last phytomer of the culm. It may be only an internode with a branch as in the panicle. It may be an internode and a sheath and blade, as in the lower culm internodes, or an internode, sheath, bud, and root, as in the rhizome. Sometimes, there is no well developed internode, and only the sheath, blade, bud, and root are prominent. Rarely, an internode, sheath, blade, root, and bud are all present as in stoloniferous shoots. We can summarize the various main combinations of the five structural elements on phytomers of various parts of the plant as follows:

Phytomer location	Internode	Sheath	Blade	Bud	Root
4th culm	Long	0	0	0	0
Lower culm	Medium	Medium-long	Medium	0	0
Panicle	Medium	0	0	Usual	0
Spikelet	Minute	Short	0	No floret	0
Crown	Minute	Medium	Short to long	Usual	Usual
Rhizome	Medium	Medium	0 to minute	Usual	Usual

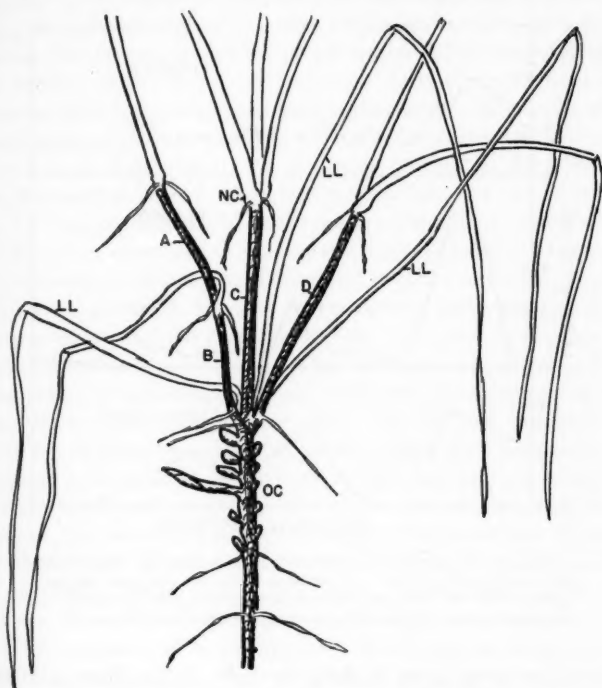


Fig. 34. In fall and spring when vegetative shoots are covered over by alluvium or manure, or by soil excavated by gophers, the internodes on the phytomers which are just maturing will develop long internodes such as A, B, C, and D, even though the leaf blades of the phytomers (LL) are long; OC, the old crown, now buried; NC, the new crown.

Intermediate combinations of the above structures may occur under special circumstances or in areas transitional between different parts of the plant. A distinctly different ratio exists between the three prominent features of phytomers (blades, sheaths, and internodes) when they are located on a rhizome, flowering shoot, and vegetative crown. Under certain circumstances these ratios can be altered by subjecting the plant to changed external conditions. If the plant is shaded, internodes will elongate in spite of the presence of leaves. This occurs in vegetative shoots which are shaded by heavy mown grass or covered by soil, as often happens around gopher mounds (text-fig. 34). Where such growth follows mowing, the growing point is raised out of the ground with the result that it is easily killed by drought, cold, or trampling.

A somewhat similar departure from normal behaviour can be noticed on rhizomes grown under special conditions. We have discussed the fact that rhizomes turn up when leaves begin to develop. If the rhizome is enclosed in a glass tube

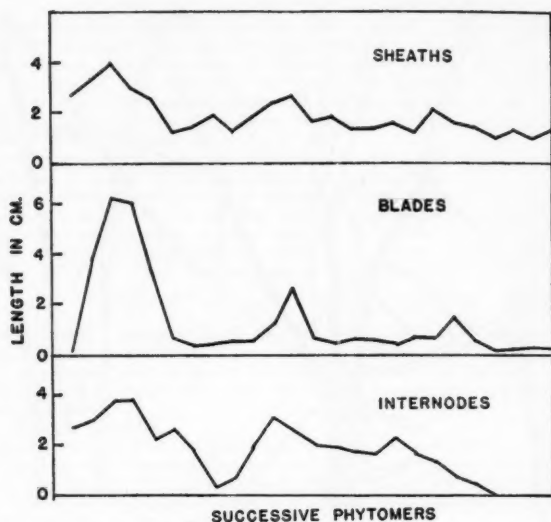


Fig. 35. A rhizome was prevented from turning up by directing it into a glass tube buried in vermiculite. The rhizome grew for several months, and was then removed and its phytomer parts measured. These measurements are shown above in the form of curves of growth.

and its leaves prevented from reaching the light, as was done in an experiment (see pl. 2), the sheaths and internodes become abnormally long. Such a rhizome is illustrated in text-fig. 35. From this diagram it can be seen that the response of the blade, sheath, and internode to the stimuli coming from the parent plant are different. While the internodes tend to respond with considerable sensitivity to prevailing conditions, the leaf blades increase in length only when the stimulus passes a certain threshold. Sheaths as usual appear to be somewhat intermediate in their reaction, embodying features of the two other organs.

The physiological basis of this manner of growth was not investigated, but the data indicate, in part, how correlations between plant parts can appear to exist at particular times and at other times to have no apparent basis in fact. It also shows that a process which normally seems irreversible can be reversed upon occasion. The trend from rhizome to shoot is commonly observed. The reverse trend is seldom witnessed or imagined possible. The reversal of differentiation in more advanced parts of the plant, as in the development of so-called viviparous shoots in the spikelet or in the appearance of leaves on the panicle, has been discussed by Sharman (1947). The mere appearance of glumes and lemmas after all leaf forms had been suppressed is also a form of reversal.

The development of any given phytomer apparently is a complicated matter which involves a great many variables operating on the plant through its physio-

logical systems. While phytomers are plastic and can be affected by environmental factors, they nevertheless eventually resolve themselves into a consistent pattern which becomes the mature plant of the proper species. This argues for some sort of internal control. Such control, however, must be of a secondary nature, since the achievement of such features of the mature plant as the inflorescence ultimately depend on environmental factors. Thus while the development of a panicle on a growing point undoubtedly affects the internode beneath it, the panicle would never have developed at all had it not been for the fact that the plant had been exposed to a certain combination of environmental conditions. Also the panicle's effect will depend on conditions of the moment and the habitat. There are thus primary environmental influences and secondary internal situations which affect the fate of a given phytomer, but they do not operate independently. Just what role the genetic material of the plant plays in this connection is not clear.

In general, it would appear that the independence of the individual structures on the grass phytomer and of the principal plant parts is more imposing than any correlations which might exist between them. Hardly any correlation can be found which can be shown to hold up under all conditions of environment. Mention has already been made of the lack of relation between leaf width and the presence of shoots. Brown (1940) found a relation between leaf width and number of rhizomes, but he sampled only two strains. The correlation of short leaves and many tillers is not dependable beyond the limits of normal domestic types. Even the correlation between culm blade length and internode length (text-fig. 27) would break down if more extreme habitat types were included. The importance of this independence of the phytomer to variation in bluegrass cannot be exaggerated. It permits a given plant or group of plants to record, in detail, the variations in its environment. It leads to an inevitable confusion in field and herbarium between induced variants and ecotypes. It likewise greatly increases the problem of recognizing and classifying strains and varieties. So-called clonal differences frequently reflect different treatment rather than different inheritance.

It is especially striking, and in the author's opinion not at all accidental, that the criteria, or combinations of criteria, which differentiate one strain or ecotype from another appear to be the very ones which are included in the repertoire of characters which can be produced by environmental manipulation or variation. The important question is why, in one case, these characters should be stable enough to be passed on to offspring, while, in the other, the same characters are theoretically only temporary. How is stability achieved?

It does not seem reasonable that this thoroughgoing similarity of induced and inherited characters should be the result of two entirely different causes. It seems more likely that morphological (and therefore physiological) response to environment and genetic change are inextricably bound together in higher plants just as they appear to be in simpler forms of life, and that drawing a line between inheritance and environment at the finer taxonomic levels is impossible.

SUMMARY

A three-year study of Kentucky bluegrass has been made with emphasis placed on the morphology and growth of the individual plant and its variation with season and environment. In addition to extensive field observations and tests, laboratory experiments and micro-dissections have been made. Previously published and unpublished work has been synthesized with these investigations in an attempt to produce as complete and readable an account of the life history of the grass plant as possible.

A grass plant is built of morphological units called phytomers. These units are produced from the growing point. They potentially consist of a leaf blade and sheath, and the internode, bud, and pair of roots immediately below this leaf. Only infrequently are all structures present and fully developed. In various combinations they unite to produce the characteristic parts of the mature plant. Ultimate simplicity is achieved in the flowering shoot where the last phytomer of the culm consists only of a much-attenuated internode.

Just as the form of the plant depends on which phytomer structures are present, so also does its growth depend on the sequence of maturation and elongation of the phytomer parts. This sequence begins with the rise of the leaf blade from the growing point, and its subsequent elongation. The leaf sheath follows, and then the internode may elongate or remain much compressed. The bud may begin to appear when the blade matures, and may develop into a shoot while the sheath is elongating or remain dormant indefinitely. Roots are usually the last structures to develop.

While the individual parts of the phytomer, and the phytomers as a whole, show considerable originality and variation, they characteristically tend to organize into three main types of shoots—the rhizome, the tiller, and the flowering shoot. These structures are analyzed with respect to their morphology and manner of growth. The basic phytomer patterns are found to hold with few exceptions.

The critical region of the bluegrass plant is the nubbin of short internodes just beneath the soil surface, to which the leaves attach and from which the three shoot types arise. This area contains the reserve supply of buds, the suppression or development of which determines what the plant will look like and what it will do.

A bluegrass plant can be interpreted on a seasonal basis, just as though it were a winter twig or a pine bough. This requires careful study of the crown area and a knowledge of progress of basic seasonal events such as flowering, tillering, and dormancy. By examining the number of phytomers, length of leaves, whether the buds develop, the position of these buds and the kind of shoots they produce, a complete picture of the year's activity can be drawn. Such a study can be used to provide an understanding of the type of plant to be expected in a given locality or habitat, under different management regimes, or in specific seasons. The structure of the crown region is of great importance in experimental tests, both laboratory and field, and statistical planning and analyses for the response obtained under

any situation will vary greatly depending on what type of plant is dominant in the experimental material.

A plan of practical management of bluegrass must first take into account to what use we intend to put it, so that we can decide what kind of a plant we need. We are then in a position to apply specific treatments to the sod. The effects of various environmental factors and treatments on grass plants have been discussed in detail with reference to their influence on specific parts of the plant.

From a taxonomic and genetic point of view it cannot be emphasized too strongly that bluegrass is flexible and that its final form is largely the result of specific environmental influences which are often brief in duration, rather remote in time, casual in distribution, and specific in effect. While under certain limited conditions correlations between various organs of the plant may exist, if populations from sufficiently diverse habitats are examined most correlations will be considerably altered and may break down completely. A study on variation in bluegrass with reference to this situation is in progress at the present time.

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EXPLANATION OF PLATE

PLATE 2

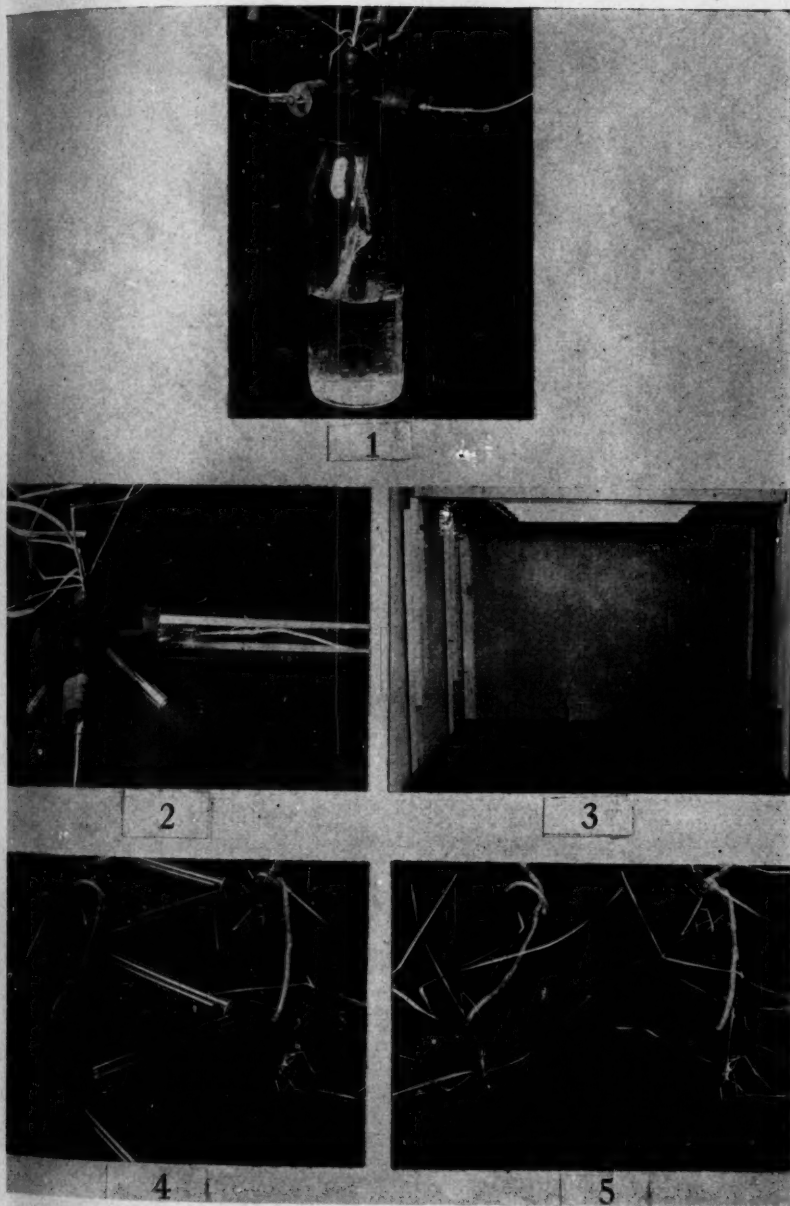
Fig. 1. Baby bottles made it possible to watch how bluegrass grows. (Some of the nutrient solution was removed to show roots and capillary tube supplying air.)

Fig. 2. Close-up of the top assembly with rhizome chamber attached and a rhizome extending into it.

Fig. 3. The bottles were placed in a light-tight box, provided with air bubbled under pressure, and the rhizome chambers concealed beneath a series of panels.

Fig. 4. One of the panels removed exposing rhizome tubes.

Fig. 5. View of the plants with panel in place.



ETTER—HOW KENTUCKY BLUEGRASS GROWS



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ETTER—HOW KENTUCKY BLUEGRASS GROWS

EXPLANATION OF PLATE

PLATE 3

Fig. 6. A confusion of long green midsummer leaves trodden into disarray by cattle.

Fig. 7. Underneath the summer grass is an equally confusing tangle of wiry stems, the rhizomes. The soil has been washed away under a stream of water.

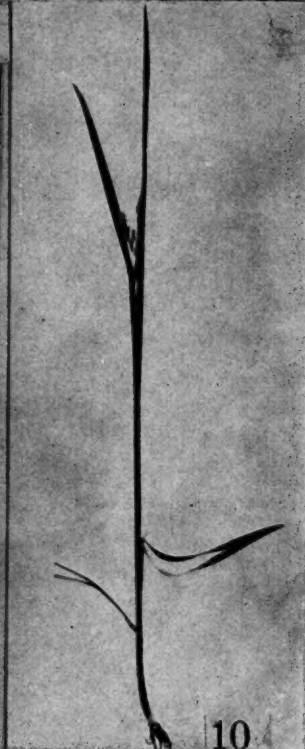
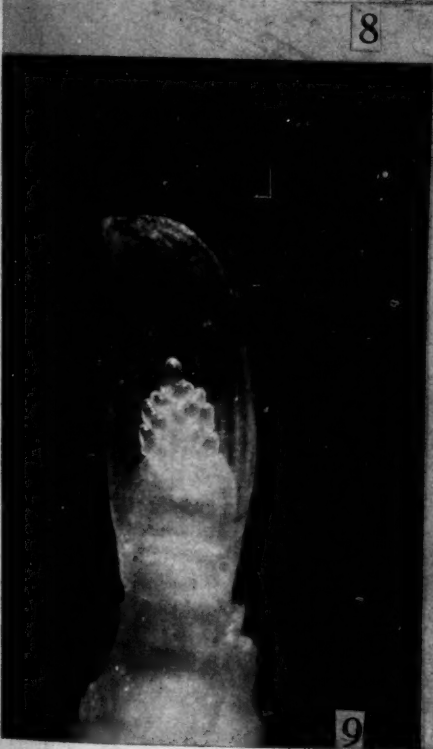
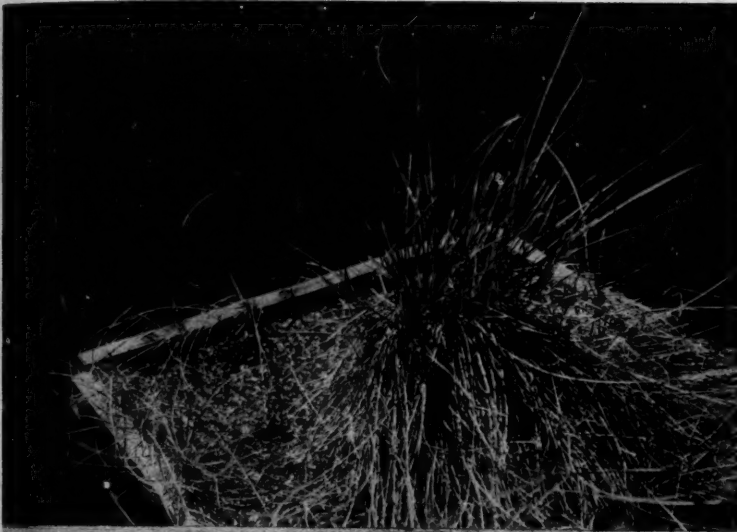
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PLATE 4

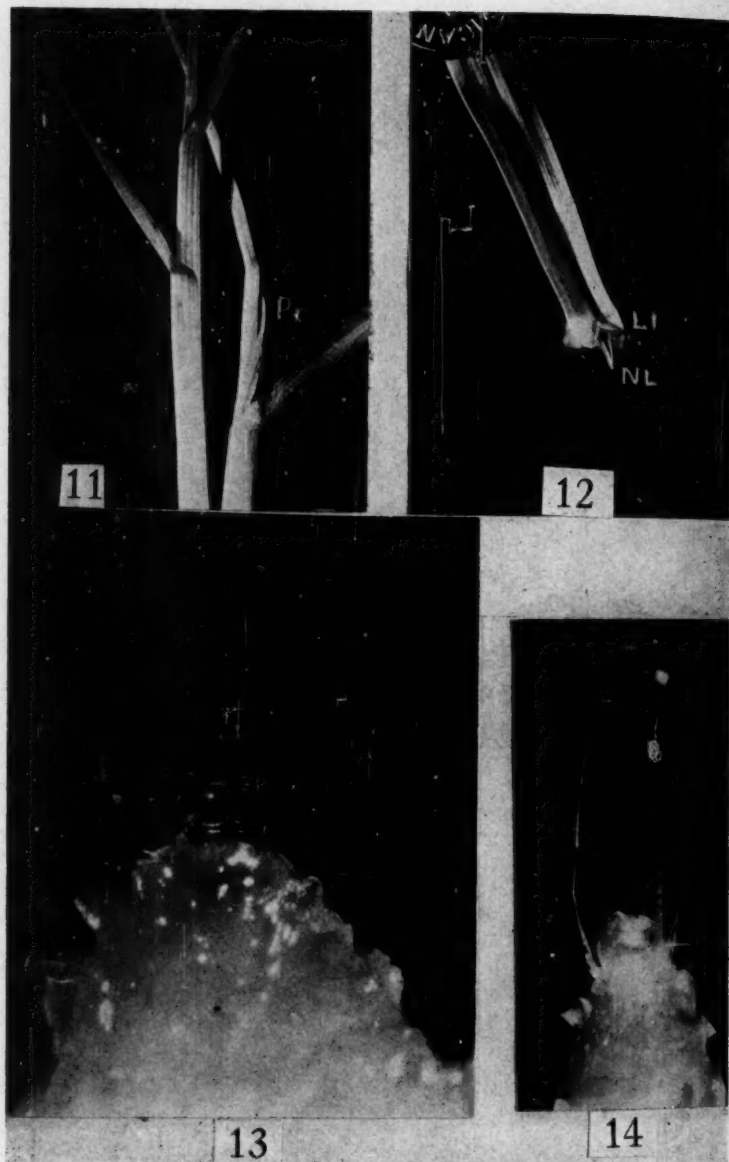
Fig. 8. A bluegrass plant and its undernourished offspring. Large parent plant has its roots in a pot of soil underneath the tray. Small plants along the left edge are turned-up rhizomes having only sterile "vermiculite" to feed on.

Fig. 9. An early stage in the development of a flowering shoot. Half of the "younger" leaf (the banded leaf in back) has been removed, showing the youngest or "hood" leaf within, and the proliferating growing point protruding through the hood. (Photo by Dr. O. T. Bonnett, of the Agronomy Department, University of Illinois.)

Fig. 10. A young flowering shoot with the panicle just appearing from its enclosing sheaths.



ETTER—HOW KENTUCKY BLUEGRASS GROWS



ETTER—HOW KENTUCKY BLUEGRASS GROWS

EXPLANATION OF PLATE

PLATE 5

Fig. 11. Successive sheaths enclose each other, but the blades bend outward at their junction with the sheath. The lowest leaf on the right clasps an intravaginal shoot with one leaf bent to the left. The prophyll marked *Pr* is still visible between them.

Fig. 12. Looking down on a bluegrass leaf. The blade is clipped with a thumb-tack, and the ligule is marked *LI* and the new blade coming up through it is *NL*.

Fig. 13. The bulbous translucent growing point of bluegrass, and two leaf primordia. (Photo by Dr. O. T. Bonnett, University of Illinois).

Fig. 14. Young leaves rising from the stem apex. Hood leaf is indicated by *HL*. (From Musgrave, 1940).

EXPLANATION OF PLATE

PLATE 6

Fig. 15. An August plant, showing rhizomes of extreme types. Left, a very abrupt, almost tiller-like shoot; right, below, a long rhizome not yet turned up. Right, above, a short arched rhizome.

Fig. 16. The tip of a rhizome. The cataphylls bend back slightly at the tip showing beginning of a very short blade.

Fig. 17. Left, the conical point of a very young cataphyll; right, the conical point has narrowed and become slit, indicating blade development has begun ($\times 80$). (From Musgrave, 1940).

Fig. 18. A series of rhizomes in various stages of turning up. Upper rhizome has formed a single tiller on the right. The crown and growing point are located just above the last roots.

Fig. 19. Rhizomes were grown in Petri dishes, some with water only (on the right), some with 1 per cent glucose (center and left). The center one died at the apex and a sprout developed from an axillary bud.



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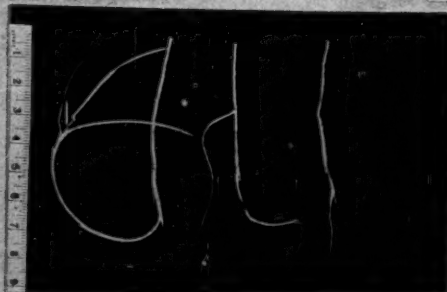
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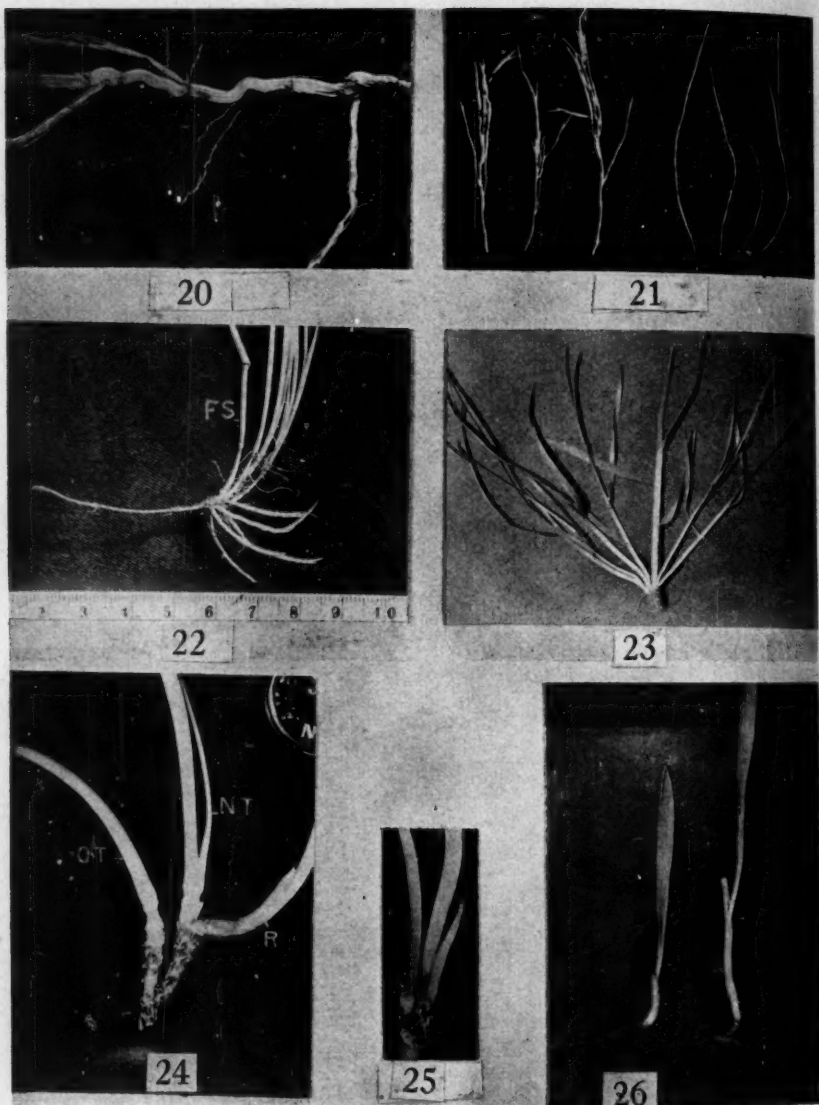


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ETTER—HOW KENTUCKY BLUEGRASS GROWS



ETTER—HOW KENTUCKY BLUEGRASS GROWS

EXPLANATION OF PLATE

PLATE 7

Fig. 20. Close-up of an old branched rhizome.

Fig. 21. Branched and unbranched rhizomes. The three on the left are from spaced plants in a nursery, the four on the right from a dense sod. (From Musgrave, 1940).

Fig. 22. Sprout rhizomes produced in August on rank meadow plant which had bloomed the previous May. FS is old flowering shoot.

Fig. 23. A bluegrass plant with five primary tillers. The main shoot is in the center. Lowest tiller on the left has given rise to a secondary shoot. The lower leaves and prophylls have been removed.

Fig. 24. Tillers arise from axillary buds. This plant shows a new tiller (NT), an old tiller of a year ago (OT), and a fairly recent short rhizome (R).

Fig. 25. The first leaf of a tiller is called the prophyll (p). It has no blade. (From Musgrave, 1940).

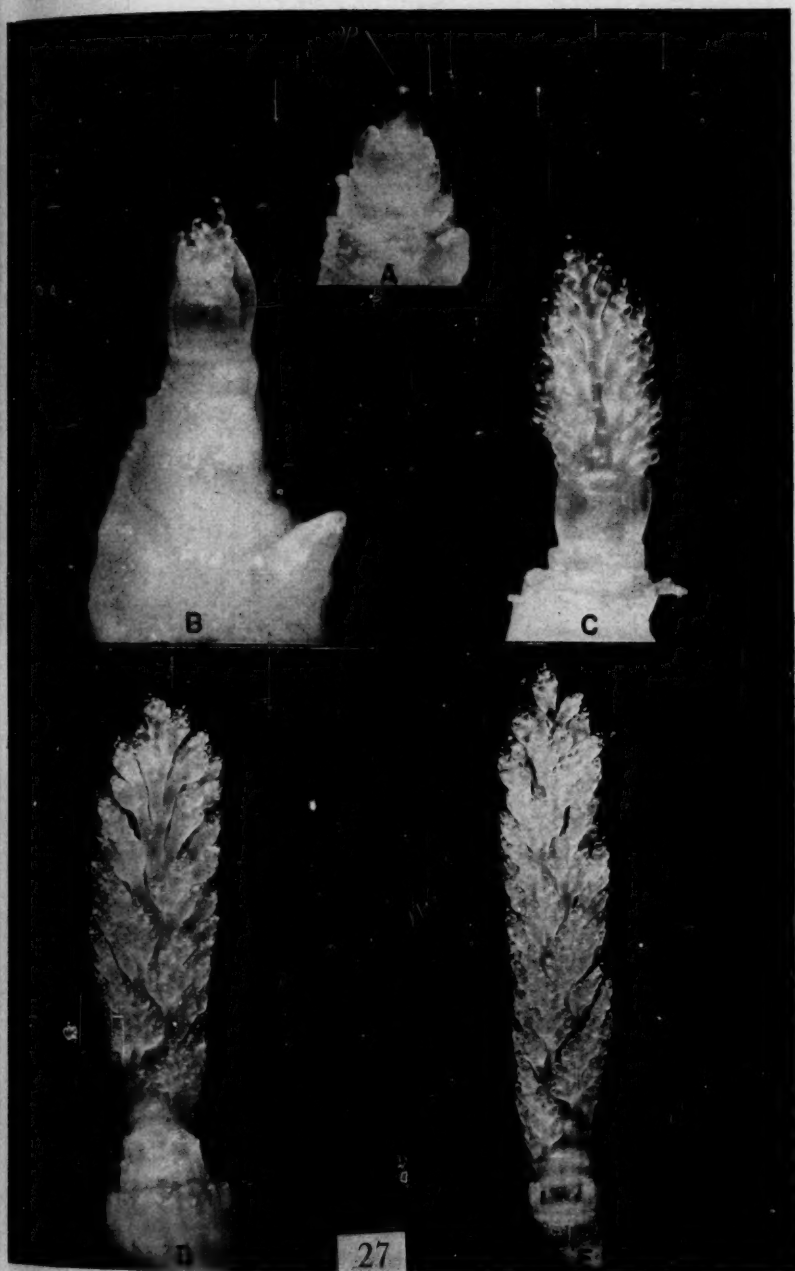
Fig. 26. Oat seedling showing the first green leaf after it has grown out of the sheathing coleoptile (C) at its base. The plant on the right shows a somewhat broken mesocotyl (M) between the grain and the first minute root.

EXPLANATION OF PLATE

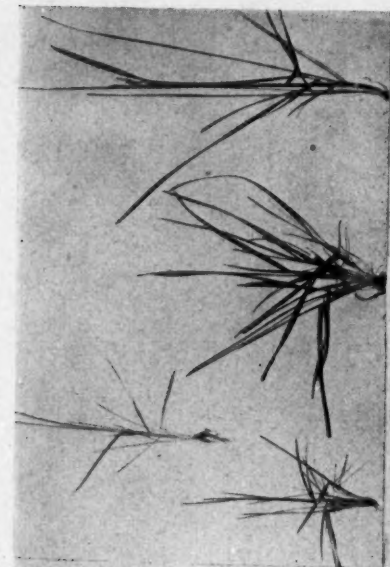
PLATE 8

Fig. 27. Successive stages of panicle development in bluegrass. (Photos by Dr. O. T. Bonnett, of the Agronomy Department, University of Illinois).

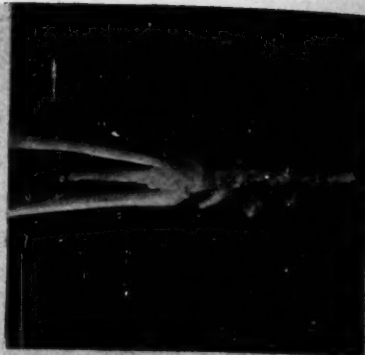
- A. The growing point elongates. (From Musgrave, 1940—compare with pl. 5, fig. 13).
- B. Proliferation begins with protuberances appearing on the growing point.
- C. The primary protuberances branch and the panicle grows very slightly.
- D. Spikelets have begun to develop.
- E. Glumes of spikelets have begun to envelop the growing points.



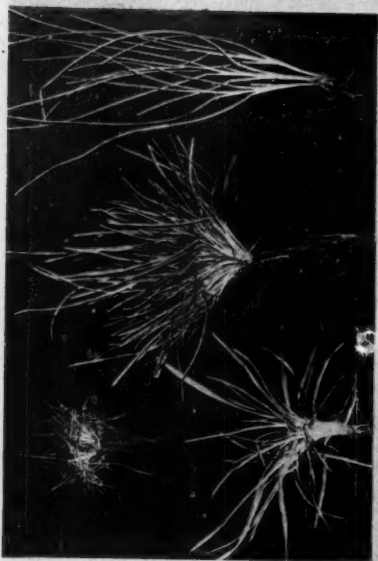
ETTER—HOW KENTUCKY BLUEGRASS GROWS



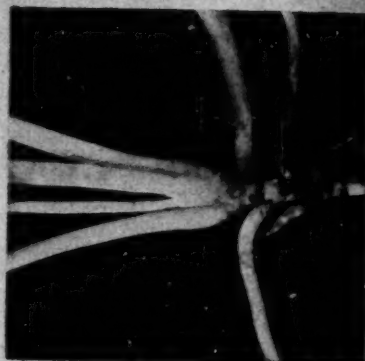
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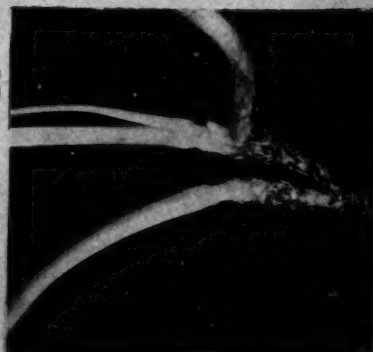
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EXPLANATION OF PLATE

PLATE 9

Fig. 28. Bluegrass plants showing various degrees of tillering. Meadow plant at right shows two primary tillers. Pasture plant at left has several secondary shoots. The plant in the center was taken from a wet spot over a buried steam pipe and has produced tillers all winter. They total about 50, and there are many of the second and third generation and a few of the fourth. Upper left, a much-tillered lawn plant with very short leaves.

Fig. 29. Plants fertilized at different times of the year with horse urine (see Table III). Upper left, control; lower left, late August; center, late October; right, January—note exertion of panicle beginning in January plant. Difference in intensity of color is also apparent in the photograph, and is true to life. Control and August plants were very pale green.

Fig. 30. Enlarged crown ($\times 3\frac{1}{8}$) of a conservative meadow plant in fall with only three buds developed in a period of a year.

Fig. 31. Crown of a more active plant from a pasture in fall showing rhizomes and tillers from late summer and fall buds.

Fig. 32. A crown with late summer and fall buds swelling in preparation for development of rhizomes the following spring. A pair of tillers at the top.

